National Bobwhite Technical Committee

WILDLIFE RESTORATION

TENNESSEE WILDLIFE RESOURCES AGENCY

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QUAIL 8: NATIONAL QUAIL SYMPOSIUM PROCEEDINGS

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QUAIL 8: NATIONAL QUAIL SYMPOSIUM PROCEEDINGS

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FOREWORD

National Quail Symposium Proceedings are a project of the National Bobwhite Conservation Initiative (NBCI), the National Bobwhite Technical Committee (NBTC), and the NBTC Science Subcommittee. At the conclusion of Quail 7 in 2012, in Tucson, Arizona, NBTC, NBCI and Dr. Patrick Keyser of the University of Tennessee (UT) announced their commitment to host Quail 8. In 2015, Tennessee Wildlife Resources Agency (TWRA) joined this effort to launch the 8th National Quail Symposium July 26–28, 2017, as a Joint Quail Conference with the 23rd Annual Meeting of NBTC, to be held in Knoxville, Tennessee, at the Holiday Inn World's Fair Park. NBTC subsequently recommended the Quail 8 Proceedings be published at the Joint Quail Conference, a daunting feat accomplished only once before for Quail V in Texas by current Quail 8 Associate Editor Dr. Stephen DeMaso.

We are pleased to announce that coincident with the publication of Quail 8, proceedings of the 1972 and 1982 National Bobwhite Quail Symposia, as well as Quail III-VII, are now published as the National Quail Symposium Proceedings in the Digital Commons Network™ (bepress™). This provides an exponential increase in dissemination of works published in the symposium series, including high quality, 100% searchable, digital copies of each paper.

The Joint Quail Conference will likely be the largest gathering, >200 participants, of biologists focused on quails, hereafter. With quail declining precipitously in abundance (e.g., near extinction of masked bobwhite as a species and northern bobwhite in Pennsylvania) and as a quarry for hunters, interest in their conservation has diminished markedly compared to 10–20 years ago when >300 participants attended national meetings. On the positive side, participants now include "non-game bird" biologists such as staff of the avian Joint Ventures and personnel of the National Park Service.

The Joint Quail Conference provides a unique opportunity for biologists to learn the latest in conservation of quails. The Quail 8 Proceedings is unprecedented among peer-reviewed quail symposia for the number of scholarly contributions—94 manuscripts and abstracts, by 72 authors, representing all species of quails in the United States, and masked bobwhite in Mexico. In addition there is a review paper on the state of the science in bobwhite translocation, and updates on the two major national quail plans, the NBCI and the Western Quail Management Plan.

The foundation and reason for the Quail 8 Symposium is the opportunity to meet colleagues. Despite the instantaneous communication of email and social media, we want to interact, just like quail enthusiasts at the First National Bobwhite Quail Symposium in 1972: the "Symposium provided an opportunity for many individuals who knew each other 'only on paper' to make face-to-face contacts and to exchange ideas on current theories and research findings." (Howard Jarrell, Secretary)

Publication of the proceedings prior to the symposium as requested by NBTC was daunting, requiring tremendous effort by the authors, 12 Associate Editors, 97 reviewers, the Science Subcommittee of the NBTC, and staff of NBCI, UT, and TWRA – all under the guidance of Allen Press, Inc. All contributed to the excellence and timeliness of the proceedings. We are indebted to many individuals, listed in the Acknowledgements, Editorial Committee, Reviewers and Steering Committee sections.

In the midst of decades-long trouble for quail populations, Dr. Leonard Brennan's concluding remarks at Quail 7 challenged professional quail enthusiasts to publish examples of success. The Quail 8 Plenary features some successes, but also lessons learned, pointing the way for improved quail conservation in the future. Quail 8 ended with Dr. Frank Thompson's look far into the future, research on the predicted effects of climate change on bobwhites. Because quail enthusiasts have worked so hard for so long to understand the species, with Quail 8 being the latest example, we are better prepared to justify conservation of quails, compared to any other species.

Although many biologists will meet face-to-face for the first time at Quail 8, because of intense peer-review over the past year, authors, reviewers and editors know each other well. Peer-review is an intense human experience, emotional at its core, fostering more dynamic discussion and interaction at the conference.

We are pleased to have collaborated with the NBTC Science Subcommittee to honor Drs. Leonard A. Brennan and Loren Wesley Burger as recipients of the Quail 8 Recognition of Excellence Award, and the late Dr. Robert J. Robel for the Quail 8 In Memoriam recognition. For Lenny and Wes an unintended consequence of distributing the Quail 8 proceedings with the conference registration was the lack of surprise at the Awards Luncheon. On the other hand, their families joined in the luncheon celebration without having to arrange travel with the usual secrets that accompany surprise announcements.

We trust the Joint Quail Conference greatly enhanced your communication with fellow professional quail enthusiasts, and that the Quail 8 Proceedings is a valuable addition to your library. Despite the new widely-available digital version, we expect the Quail 8 original rendition of quails of the U.S.A. will ensure this proceedings is displayed prominently in your office.

With the completion of this symposium, we are hopeful for a continued future of management success, research, and dedication for sustaining the quail species of our continent. Most importantly, we look forward to Quail 9 in 2022.

—Tom Dailey and Roger Applegate, Editors

ACKNOWLEDGMENTS

The Quail 8 proceedings and symposium required a small army to be successful. At this writing 5 weeks before the symposium, some key people could be missed in the proceedings acknowledgements, and similarly, institutional contributions in some cases will not be finalized until after Quail 8. Final formal recognition of individuals and institutional contributors will be announced at the meeting and published in the program and on the web site. The formal roles of many of the recognized individuals below, and their affiliations, are listed in the Joint Quail Conference Committees page. Quail 8 was made possible by contributions by the following individuals, listed in roughly chronological order of their contribution to the proceedings, symposium, and Joint Quail Conference.

Quail 8 is part of a series that began in 1972, tying biologists together over decades and across the country. The location in Tennessee was supported by the previous chairs of National Quail Symposia, Dr. Leonard Brennan (Quail IV), Dr. Stephen DeMaso (Quail V), and Dr. John Carroll (Quail 6/Gamebird 2006), and was conceived by Dr. Pat Keyser, University of Tennessee, who announced Tennessee as the host at the Seventh National Quail Symposium in Tucson, Arizona, on January 12, 2012. I relied on the guidance and participation of Lenny, Steve and John, partly for Quail III in 1992, and in 2009 for the transfer of the quail proceedings series to the National Bobwhite Technical Committee (NBTC) and National Bobwhite Conservation Initiative (NBCI), beginning with Quail VII. Together we also agreed to transform the entire series' proceedings to the e-journal, National Quail Symposium Proceedings, forever improving dissemination of each author's publications.

The joining of Quail 8 with the 23rd Annual Meeting of the National Bobwhite Technical Committee (aka, Joint Quail Conference), was supported by NBTC Chairs Chuck Kowaleski and John Morgan, the NBTC Steering Committee, NBCI Director Don McKenzie, and Roger Applegate, Mark Gudlin, and Timothy White of the Tennessee Wildlife Resources Agency.

Collaboration on the Quail 8 proceedings with editors Roger Applegate and Kathleen Ingraham (Allen Press, Inc.) has been transformative in key ways, including frequent editing decisions small and large, and Allen Press's Quail 8 PeerTrack™ online manuscript system. We talked weekly since fall 2016; we have been a great team. Business expertise for the proceedings was provided by Penny Barnhart, and Julia Mitchell and John Aamot of Allen Press, Inc.

The Quail 8 technical program's excellent and diverse quality resulted from leadership by Roger Applegate, Beth Emmerich (NBTC) and Dr. Kelly Reyna (NBTC). Roger also led organization of program moderators, and Beth and Kelly led the Quail 8 Recognition of Excellence and In Memorium programs. Implementation of Quail 8 products, communication, and services resulted from hard work by Penny Barnhart, Alyssa Merka, Molly Foley and Michele Wilson. Derek Evans and Kenneth Duren (former NBCI staff) established the foundations for communication and organization of Quail 8.

The National Quail Symposium Proceedings e-journal was conceived and implemented by Dr. Rachel Caldwell, University of Tennessee Libraries, graduate student Nick Guernsey, and Alyssa Merka, and guided by decisions by Roger Applegate, Beth Emmerich, and Dr. Kelly Reyna.

The Quail 8 proceedings, timely and of excellent technical quality, required expert communication and technical analysis by the associate editors, working with reviewers and authors (see Reviewers section). The institutes providing in-kind support of Quail 8 via work by Associate Editors are listed in the Institutional Contributors section. Quail 8 Associate Editors included the following individuals: Roger Applegate, Dr. Leonard Brennan, Dr. Brad Dabbert, Dr. Thomas Dailey, Dr. Stephen DeMaso, Kenneth Duren, Dr. Dwayne Elmore, Dr. Joseph (TJ) Fontaine, Dr. Robert Gates, Dr. James Martin, Dr. Mark McConnell, Dr. Theron Terhune, and Dr. Christopher Williams.

The Quail 8 proceedings cover is beautiful and unique among the quail series for representation of the six species of quails in the United States and the sub-species, Masked Bobwhite. David Besenger, a Missouri artist (also the illustrator for Quail III), crafted the 2.5-D images of the quails, and generously donated the copyrights to NBCI. Michael Wifall, an Arizona photographer, donated the Smoky Mountains photo. Alyssa Merka supervised and designed the covers.

The technical program's quality owes much to the invited authors, including Casey Cardinal, Dr. Brad Dabbert, Beth Emmerich, Dr. Eric Grahmann, Dr. James Martin, Don McKenzie, John Morgan, Dr. Frank Thompson, and Dr. John Yeiser.

The technical program was supported by national wildlife leaders. Larry Kruckenberg, Executive Secretary, Western Association of Fish & Wildlife Agencies (WAFWA), ensured the National Quail Symposium would be a priority meeting for western state wildlife agencies, including designation as a WAFWA-sanctioned technical workshop. Larry also was the catalyst for participation in Quail 8 by the WAFWA Western Quail Working Group. David Haukos, Editor-in-Chief, Wildlife Society Bulletin, provided the author publication guidelines of The Wildlife Society for use by Quail 8.

The implementation of the Joint Quail Conference, including preparation and follow-up business, was made possible by a dedicated team of individuals under the leadership of the steering committee (see Committees section for details), including the following: Danny Akins, Roger Applegate, Penny Barnhart, Clint Borum, John

Doty, Andy Edwards, Molly Foley, Alyssa Merka, Melissa Raulerson, Stacy Saxton, and Timothy White.

Funding for Quail 8 was procured through the efforts of the following individuals: Roger Applegate, Dr. Lenny Brennan, Dr. Wes Burger, Dr. Brad Dabbert, Andy Edwards, Thomas Franklin, Galon Hall, Chuck Kowaleski, Don McKenzie, John Morgan, Robert Perez, Dr. Kelly Reyna, Dr. Dale Rollins, Dr. Theron Terhune, and Timothy White.

Please join me in extending a hearty thank you for a job well-done to each of these individuals.

INSTITUTIONAL CONTRIBUTORS

Institutional support of Quail 8 was essential to the publication of the proceedings and to ensure a high-quality experience for symposium participants. At this writing five weeks before the symposium, contributions in most cases will not occur until after the proceedings is printed, and thus, final recognition of contributors will occur at the event and be published in the program and symposium website.

Quail 8 was built on the funding foundation of the National Bobwhite Conservation Initiative, the Tennessee Wildlife Resources Agency, the University of Tennessee, the Federal Aid in Wildlife Restoration Program, the National Bobwhite Technical Committee, and participating stage wildlife agencies.

Leading financial contributions are being provided by the United States Department of Agriculture Natural Resources Conservation Service, Caesar Kleberg Wildlife Research Institute, National Bobwhite Technical Committee, and Tall Timbers Research Station and Land Conservancy.

Contributions of funding, service, and in-kind support for staff working on editorial and organizational committees, in alphabetical order, included: Caesar Kleberg Wildlife Research Institute, Gulf Coast Joint Venture/United States Fish and Wildlife Service, Mississippi State University Forest and Wildlife Research Center, Oklahoma State University, Quail Forever, Rolling Plains Quail Research Ranch, Tall Timbers Research Station and Land Conservancy, Tennessee Wildlife Resources Foundation, Texas Tech Quail Tech Alliance, The Ohio State University, the UNT Quail Program at The University of North Texas, University of Delaware, University of Georgia, and University of Nebraska/United States Geological Survey.

—Dr. Thomas Dailey, Chair, National Quail Symposium Technical Committee

RECOGNITION OF EXCELLENCE AWARD RECIPIENTS

The National Bobwhite Technical Committee Science Subcommittee led the programs for the National Quail Symposium Recognition of Excellence Award(s) and In Memorium recognition for the Eighth National Quail Symposium. These programs are described in detail on the symposium web site. The awards and recognition were presented during the Quail 8 banquet awards luncheon on Friday, July 28, 2017. Each award recipient received a fine art print of the Quail 8 Proceedings cover with an engraved plaque recognizing their unique contribution to quail science.

DR. LEONARD “LENNY” A. BRENNAN

Dr. Brennan is currently a professor and endowed chair for quail research at Caesar Kleberg Wildlife Research Institute and Department of Animal and Wildlife Sciences, Texas A&M University, Kingsville, where he has been since 2001. Prior to this position, he was the Director of Research at Tall Timbers Research Station in Tallahassee, Florida. During his career, he has worked with mountain quail in the West and bobwhites in the Southeast and Texas. He coordinated and edited the first-ever national quail plan at the Quail III Symposium. He served as editor of the Quail IV proceedings and Associate Editor for Quail VII and this (Quail 8) proceedings. He has served as the academic representative to the Steering Committees of the Southeast Quail Study Group and the National Bobwhite Technical Committee and has been an active member of those groups since their inception. He edited the book, Texas Quails: Ecology and Management, which received the 2008 Outstanding Edited Book Award from The Wildlife Society and several other awards. He led the first ever Wildlife Society Quail Symposium at the 2014 Annual Wildlife Society Meeting. Lenny has served as the Editor-in-Chief and as an Associate Editor of The Journal of Wildlife Management and Editor-in-Chief of The Wildlife Society Bulletin. He has authored or co-authored more than 180 scientific publications and more than 100 extension and popular articles. The results of Dr. Brennan’s research on bobwhite and their management have greatly increased our knowledge and understanding of this iconic species.

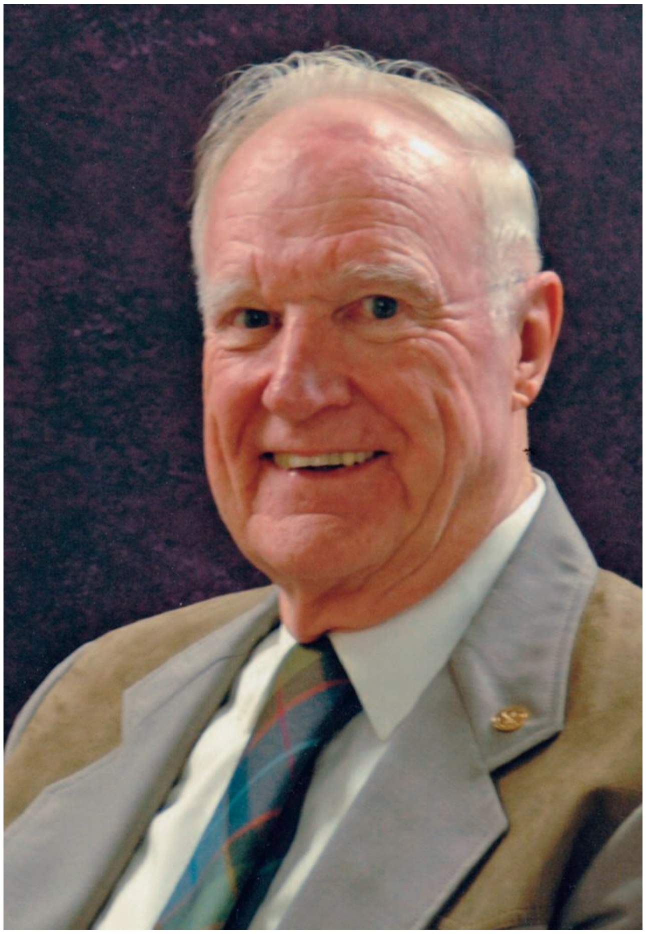
DR. L. WES BURGER, JR.

Dr. Burger is currently the associate director of the Mississippi State University Forest and Wildlife Research Center and the Mississippi Agricultural and Forestry Experiment Station in Starkville, Mississippi. He has been a member of the former Southeast Quail Study Group, and the current National Bobwhite Technical Committee since their inception, and had an integral role as chair and member of the Science Subcommittee for over a decade. Wes has served leadership roles in the Southeastern Association of Fish and Wildlife Agencies' Southeastern Bobwhite Technical Committee, Midwest Bobwhite Research Initiative, Ames Plantation Quail Task Force, board member for the Tall Timbers Research Station, Natural Resources Conservation Service (NRCS) Conservation Effects Assessment Project, and the North American Bird Conservation Initiative. He worked with the Southeast Quail Study Group to develop and implement the NRCS Bobwhite Restoration Project and National Conservation Practice (CP) 33 Monitoring Program. He has authored or co-authored 14 book chapters, 52 symposia proceedings, and 90 peer-reviewed scientific publications, with much of his work focused on bobwhite ecology and management. From his early research on bobwhite mating strategies and thermoregulation, to more recent work in applying Farm Bill conservation programs to enhance bobwhite and other wildlife populations, Dr. Burger has the ability to translate ecological knowledge to on-the-ground quail management. His work has helped develop and refine Farm Bill conservation practice standards to benefit wildlife populations which have great potential to improve bobwhite habitat throughout their range.

—Beth Emmerich, Science Subcommittee Chair, National Bobwhite Technical Committee, and the Quail VIII Program Committee

IN MEMORIUM

ROBERT "BOB" J. ROBEL 1933–2013



Robert J. Robel was born in 1933 in Lansing, Michigan. He was accepted into medical school at Michigan State University when he was a senior in high school. He changed his major from pre-medicine to wildlife ecology his junior year because he did not want to be stuck in an office. He put himself through college with a taxidermy business he purchased as a sophomore in high school. During his undergraduate career, he sought out advisors and secured funding at the University of Idaho and Utah State University where he received his master's and doctoral degrees.

He was hired as an assistant professor at Kansas State University's Department of Zoology in 1961. He traveled to the United Kingdom to study black grouse in 1967 on a Fulbright Scholarship. Much of Robel's research in Kansas was devoted to upland game birds, specifically prairie chickens and northern bobwhites. His research greatly increased our understanding of their behavior, habitat needs, and management. He also helped establish the Kansas Cooperative Fish and Wildlife Research Unit at Kansas State University. In his 50 years as a faculty member in the Division of Biology, he mentored hundreds of students who have gone on to successful careers in the wildlife field. His body of work involved habitat use, food habits, bioenergetics, and effects of herbicides. Results of his and his students' research have resulted in over 250 peer-reviewed publications. His research examining visual obstruction measurements and the weight of grassland vegetation gave scientists a quicker, easier way to evaluate vegetation density important for understating relationships of grassland birds and their habitats with what is now known as the "Robel Pole Method." Dr. Robel was a consultant and science advisor for several Kansas governors, energy companies, and served on many committees and task forces. He was also on a federal advisory committee for the Department of the Interior concerning wind power and wind farms.

Bob began competitive shooting while still in high school, and holds numerous regional and state championship titles in skeet and rifle shooting from Michigan, Idaho, and the Midwest. He served as the U.S. Olympic shooting team chairman, served on the Board of Directors for the National Rifle Foundation for 25 years, and was very active with the Kansas State Rifle Association. He received many awards throughout his career, including the Centennial Distinguished Alumni Award from the University of Idaho, and was inducted into their Alumni Hall of Fame in 1997. In 2001, he received the Lifetime Achievement Award from the College of Natural Resources Alumni Association at Utah State University. He received the Governor's Conservationist of the Year Award, the Proud Kansan Award from the Outdoor Writers Association, and the Outstanding Professional Award from the Kansas Chapter of the Wildlife Society.

—James Pitman, Conservation Services Director, Lesser Prairie Chicken Initiative, Western Association of Fish and Wildlife Agencies, and former student of Bob Robel

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CLOSING REMARKS

TRANSLOCATION AS A POPULATION RESTORATION TECHNIQUE FOR NORTHERN BOBWHITES: A REVIEW AND SYNTHESIS

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) abundance has declined precipitously for decades across much of the species range, to the point of widespread local, regional, and statewide extirpation. Because of successful translocations of other gallinaceous birds, bobwhite enthusiasts increasingly call for use of the approach. Consequently, the National Bobwhite Technical Committee (NBTC), on behalf of state agencies, requested a review and recommendation by the NBTC Science Subcommittee. Thus, our paper is co-authored by invited experts and includes reviews of peer-reviewed publications, manuscripts in these proceedings, state agency reports, experience by co-authors, and a survey of perspectives on translocations by state wildlife agency members of the NBTC. We discuss the state of science on key aspects of bobwhite conservation, offer best management practices (BMPs) for using translocation as a potential bobwhite restoration technique, and suggest ways to reduce uncertainty about implementation. We note that although conservationists

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operate on a relatively solid foundation of improving bobwhite abundance via increased quantity, connectivity, and quality of habitat, population restoration success to- date is relatively rare *and* unpredictable. Similarly, some past translocations have been unreliable with an abundance of failures and inadequate experimental designs. We conclude that because of major uncertainties regarding habitat, population phenomena (e.g., Allee effect) and restoration techniques, outcomes of translocations remain unpredictable; thus, future efforts must be a part of sound and rigorous peer-reviewed research. To improve scientific efforts, we recommend the following BMPs for future translocations: (1) target bobwhite abundance should be >800 post-translocation which will likely necessitate ≥600 ha of suitable and accessible habitat while a larger (e.g., >800 ha) area will be needed in areas with lower carrying capacity and when sites are highly fragmented or isolated, (2) personnel should identify and avoid stressors to bobwhites in all phases of the translocation process (i.e., capture, holding, transportation, and release), (3) source populations should be disease free and from similar environments and latitude; preferably from the nearest suitable source, (4) conspecifics should be present on recipient sites (5) birds should be released just before the breeding season (i.e., March or April), and (6) the translocation should incorporate robust short- and long-term bird (i.e., abundance and/or density) and habitat monitoring efforts (i.e., the Coordinated Implementation Program (CIP) of the National Bobwhite Conservation Initiative (NBCI)). In conclusion, we note that translocation of bobwhites is not a panacea for broad scale restoration of bobwhites; however, the technique should remain at the forefront of bobwhite science, taking into account knowledge of the species' life history and ecology, so that a practical and reliable solution can be developed. We recognize this paper is just the beginning of vigorous debate, testing of concepts, and on-the ground implementation of successful bobwhite conservation.

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Key words: Allee effect, *Colinus virginianus*, northern bobwhite, population restoration, reintroduction, restocking, translocation

INTRODUCTION

Northern bobwhites (*Colinus virginianus*) have experienced precipitous range-wide population declines averaging 3.28% annually since 1966 (Sauer et al. 2017) and has been attributed to myriad reasons including habitat loss, fragmentation, and degradation (Hernández et al. 2013). Despite conservation and restoration efforts (Dimmick et al. 2002, National Bobwhite Technical Committee 2012) populations continue to decline at alarming rates (Sauer et al. 2017). The fundamental objectives of most state agencies and the National Bobwhite Conservation Initiative (NBCI) are to achieve populations that can sustain a recreational harvest and persist in perpetuity. To this end, managing habitat has been the *modus operandi* with mixed success with very few published success stories (e.g., Morgan et al. 2017) and plenty of cries of frustration. The lack of success at large spatial scales has instigated the use of population restoration techniques (PRT) to re-establish self-sustaining populations. Population restoration techniques include reintroductions through translocation of wild bobwhites, restocking through translocations of wild bobwhites or artificially propagated birds, and on rare occasion conservation introductions (i.e., introduction bobwhites beyond their traditional range; Seddon 2010). It is important to establish definitions of these terms, as linguistic uncertainty exists in the bobwhite community. We will use Seddon's (2010) terminology because it facilitates consistency between bobwhite conservationists and other conservation communities. *Reintroduction* of bobwhites entails the release of bobwhites into an area that was once part of its range but has since been extirpated (IUCN/SSC 2013, Seddon 2010). Whereas *restocking*, reinforcement, supplementation, or augmentation (all synonyms) refers to the release of bobwhites into an existing population of bobwhites (Maguire and Serveen 1992, Seddon 2010). Lastly, *translocation* is the physical process of moving birds from source to donor site. Reintroductions and restocking efforts both require translocation and have been duplicated throughout the bobwhite range with varied outcomes. Additionally, success has been defined in a myriad of ways and an operational definition of success for bobwhite PRTs is needed.

The International Union for Conservation of Nature (IUCN) *Guidelines for the Re-Introduction of Galliformes for Conservation Purposes* recommends defining success in three phases, "the survival of founders, evidence of breeding by founders, and long-term persistence of the translocated population" (World Pheasant Association and IUCN/SSC Re-introduction Specialist Group 2009). Short-term goals may include survival of translocated bobwhites and successful production. Long-term goals would include the persistence and growth of the population, to the point that it becomes self-sustaining and could withstand hunter harvest without significant reduction to the population size. This long-term condition defines the ultimate success for bobwhite population restoration. However, an operational definition of success is needed.

Following the NBCI Coordinated Implementation Program (Morgan et al. 2016), if the population reaches the prescribed population goal in 10 years [i.e., 800 bird minimum *sensu* Guthery et al. (2000)] and stabilizes ($\lambda = 1$), the reintroduction or restocking effort would be considered an operational success. The necessity of PRT to achieve this operational success is conditional on population phenomenon (e.g., Allee effects; explained below) and the use of PRT in the absence of necessity to reach the critical threshold is beyond the scope of this manuscript (i.e., Allee effects in bobwhites is a hypothesis that needs to be tested). Operating under these premises, we offer a theoretical, empirical, and frankly expert opinion-based review of the literature such that PRT may be implemented, under current best management practices, knowing future research and monitoring will continue to improve these practices. This paper was crafted to meet a specific request by the National Bobwhite Technical Committee (NBTC), and was conducted under the leadership of the NBTC Science Subcommittee (National Bobwhite Technical Committee 2015). The choice to implement translocation or allow it ultimately belongs to the state agency per the Public Trust Doctrine. Our goal is to provide those decision makers the current science as to inform their decision.

WORKING HYPOTHESIS FOR OPERATIONAL SUCCESS CRITERIA

Bobwhite populations can exhibit fast population growth rates in initial phases of restoration but still may take many years to reach the critical threshold. The 10-year condition is an assumption based on theory of population dynamics, some empirical data, and a few key assumptions that need to be tested. No population grows to infinity forever and should reach a stable equilibrium point. The simplest expression that creates a stable equilibrium population size is the logistic equation (Case 1999). The continuous logistic equation is defined as,

$$\frac{dN}{dt} = rN(\frac{K-N}{K})$$

where r is the intrinsic population growth rate, N is population size, and K is carrying capacity. Note, if $N = K$, the rate of change for the population ($\frac{dN}{dt}$) will become zero. Heuristically, this equation provides a starting point to determine how long it may take a reintroduced population or restocked population to reach the 800 bird critical threshold. If we assume that fall carrying capacity is 2.47 bird ha^{-1} and an 800 ha tract of land, then the stable population equilibrium is 1,946. Then how long it takes a population to get to that point is a function of N_0 (initial population size) and the intrinsic rate of growth (r). For reintroduced populations, N_0 is the number of birds initially translocated. If 0.35 birds ha^{-1} (average number translocated by Sisson et al. 2017) were reintroduced the N_0 is 287 birds. Using anecdotal and empirical growth rates (Morgan et al. 2017, Sisson et al. 2017; McConnell 2016) during the initial phases of restoration the population can take anywhere from 5 years ($r = 0.40$) to 16 years ($r = 0.10$; Figure 1). Obviously translocating more birds to increase N_0 could speed up the population reaching the critical 800-bird threshold, but the supply of wild bobwhites is limited and we are assuming survival and reproduction by translocated birds. This simple exercise also demonstrates the importance of long-term monitoring to determine success—determining failure or success after a few years is premature. An important caveat to consider is this mechanistic model does not take into consideration "black swan" events that cause unexpected population crashes (Anderson et al. 2017). Environmental stochasticity and severe weather events would cause the populations to take longer to reach the critical threshold or cause local extirpation (e.g., Errington 1933, Roseberry 1962, Burger et al. 1995, Wiley and Stricker 2017, this volume; and as discussed later in the paper). Nonetheless, this conceptual framework gives credence to the 10-year period for determining operational success and a working hypothesis as to how bobwhites may respond to PRT.

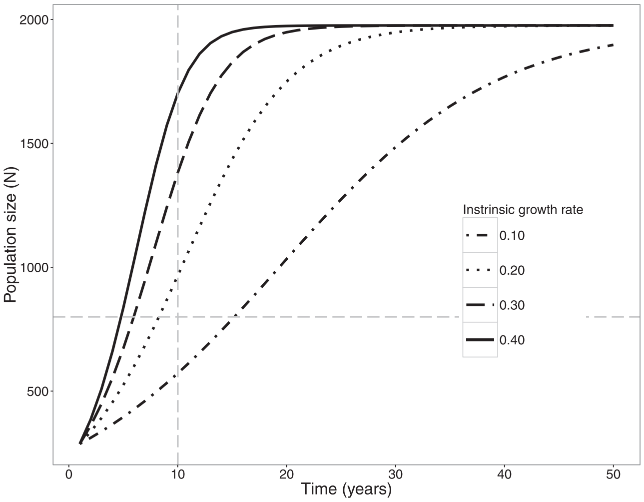

Fig. 1. Hypothesized response of northern bobwhite (*Colinus virginianus*) to reintroduction based on a continous logistic growth model with N_0 (initial population size) being 287 bobwhites in the spring (based on Sisson et al. 2017) and four possible intrinsic growth rates (based on Sisson et al. 2017 and McConnell et al., unpublished data). Carrying capacity was assumed to be 2.27 birds ha^{-1}. The vertical line at 10 years signifies the assumed expectation that success should be achieved by that time and the population monitored until then. The horizontal hashed-line represents the critical population threshold of 800 birds (Guthery et al. 2000) needed to determine success.

There are a few examples of successful, in the short-term, reintroductions in the bobwhite literature as discussed later in this review, but *reintroduction of bobwhites* has been unsuccessful (see below). Conversely, species establishment, reintroduction, and range expansion, have been notably successful for ptarmigan (*Lagopus* spp.), gray partridge (*Perdix perdix*), wild turkey (*Meleagris gallopavo*), and ring-necked pheasants (*Phasianus colchicus*) (Allen 1956, Griffith et al. 1989, Dickson 1992, Kimmel and Krueger 2007, Braun et al. 2011). As reviewed by Braun et al. (2011), all 12 species of grouse in North America have been translocated, with both success and failure. Successful movement from place-to-place of grouse and wild turkey was largely dependent on suitable unoccupied habitat. Braun et al. (2011) provided 15 recommendations for successful translocation of ptarmigan, and perhaps the most important, summing up all aspects of a well-executed translocation project, is the need to report results in a peer-reviewed publication. Similarly, Germano et al. (2015) concluded that translocations for many species fail to follow scientific best practices and are poorly documented, limiting learning, and improvement.

Much of the translocation parlance among bobwhite conservationists refers to restocking. Restocking, aims to augment a population to "avoid a critically low population size threshold… [to avoid] genetic or demographic collapse due to stochastic events (Seddon

2010).” The critical thresholds for bobwhites have not been empirically derived but Guthery et al. (2000) and Sands et al. (2012) provide guidance based on simulations (discussed more later). Restocking efforts via artificially propagated bobwhites are universally futile (e.g., Buechner 1950, Fies et al. 2000, Kinsey et al. 2012) and reviewing that literature is beyond the scope of this review. However, restocking bobwhites through the translocation of wild bobwhites has been successful in the short-term (Terhune et al. 2006b) and long-term (Terhune et al. 2010 and reevaluated 10 years later in Sisson et al. 2012). Of the many historical efforts to restock via translocations, a few recent studies have demonstrated success as indicated by survival and reproduction not less than that of resident birds (Jones 1999, Terhune et al. 2006b, 2010). A later translocation study also conducted in Georgia resulted in a 115% population increase on the treatment area (Terhune et al. 2010) which has been shown to stabilize at >1.25 birds per acre more than 13 years later (see Sisson et al. 2017 [this volume]). Furthermore, these studies demonstrate that *translocation* per se does not affect the survival of those birds (i.e., they survive the move quite well) under certain conditions being met as outlined in Terhune (2008) and Terhune et al. (2010). These case studies demonstrate that the survival, reproduction, site fidelity, and fecundity of translocated bobwhites are sufficient to allow short-term persistence (e.g., 2-5 years) and in one case long-term persistence (Terhune et al. 2010, Sisson et al. 2017 [this volume]). Many of these studies, did not have a control site (paired site without the addition of bobwhites), and where there was a control (see Terhune 2008 Terhune et al. 2010, Sisson et al. 2017 [this volume]) it cannot be said with certainty that restocking was necessary for the population to reach the critical thresholds (Guthery et al. 2000). Put another way, we cannot say for sure that the population would not have increased in the absence of translocation (Downey et al. 2017). However, this does not relegate the fact that translocation did not negatively affect bobwhite demographics and was potentially an impetus for more rapid population growth (Terhune 2008, Sisson et al. 2017 [this volume]). Stakeholders often want immediate results following habitat restoration efforts and restocking can provide, at least in the short-term, positive population responses and stakeholder satisfaction as well as encourage management on the premise they will receive wild birds through translocation (Sisson et al. 2017).

Not all restocking efforts have been successful, but inferences from many of these efforts are limited because they are confounded in some way. Scott et al. (2013) investigated restocking by translocating wild bobwhites into fragmented landscapes. The effort was unsuccessful. Their results are unsurprising considering fragmentation at the ecoregion scale was the presumed cause of the low bobwhite abundance; therefore, any population restoration efforts without alleviating the cause of the original extirpation will have a high probability of failure. This incongruence between a conservation action (i.e., restocking) and the management implications derived from research is an impetus for this review. The scientific community needs to provide sound and rigorous experimental tests of reintroductions and restocking efforts. Moreover, reasons for doing PRT and constraints on using PRT are plentiful and need to be discussed in detail. Furthermore, there is a need to reduce the uncertainty regarding reintroductions and restocking such that past mistakes can be avoided. Pragmatically, several states are considering PRT as ways to restore bobwhite populations and need information to make an informed decision. Pennsylvania Game Commission was one of the first state agencies to declare statewide extirpation of bobwhite (NBCI 2015:46).

HISTORICAL TRANSLOCATION EFFORTS

State wildlife agencies have extensive experience translocating wildlife, and a review of select efforts for bobwhite follows. The list excludes results of studies where the focus was release of first-generation progeny (F1) (e.g., Roseberry et al. 1987, Fies et al. 2000). A non-exhaustive list of projects is listed in chronological order.

Wisconsin, public land, initiated in 1950. Kabat and Thompson (1963:127) reviewed a long history of translocation, across many areas, usually undertaken to remedy winter-caused population declines, perhaps local extirpation in some cases. They emphasized the decline of suitable habitat in the species’ range and concluded translocation of wild bobwhite produced mixed results, including no reproduction, reproduction for 1-2 years, and dispersal toward existing native populations.

West Virginia, public land, initiated in 1990. Framed as a pilot study, in collaboration with a local chapter of Quail Unlimited, Inc., 63 bobwhites from Kansas were released, some with radio transmitters, into an area with 28 hectares of suitable habitat. A small fraction of the bobwhites could be found in 1992. Crum (1993) pointed out the habitat was less than optimal for bobwhites and recommended that further stocking in West Virginia not be attempted.

Indiana, public and private farmlands in northern Indiana, initiated in 1990. The impetus for translocation was to remedy winter-caused population declines, perhaps local extirpation in some cases. Local chapters of Quail Unlimited, Inc. provided extensive support. Osborne et al. (1993) suspected radio transmitters on released birds caused mortality, and subsequently Frawley (1999) used breeding season surveys to determine bobwhite population response. During 1993-1995, Indiana Division of Fish and Wildlife released 868 wild bobwhites on 44 sites widely distributed across northern Indiana, and subsequent call counts on control and release sites indicated elevated abundance for 2-3 years after translocation, but then a sharp decline, and eventually insignificant difference between control and release sites. Frawley (1999) concluded that longer-term monitoring was needed to determine if the observed short-term increased abundance on released sites is sustainable, and lacking any identification of individual released birds, could not conclude that birds existing in 1998 were the progeny of translocated bobwhites.

Texas, Rio Grande Plains ecological region, initiated in 1993. Perez at al. (2002) studied resident and translocated bobwhites and compared survival of radio-tagged birds. Translocated birds died at a higher rate, i.e., 50% loss in 47 days vs. 72 days for residents, and at 12 weeks, their survival was not significantly different.

Tennessee, private land, initiated in 1994. Jones (1999), collaborating with the Tennessee Wildlife Resources Agency, studied radio-tagged resident and translocated bobwhites and compared their survival and movements. During 2 years of research, population performance was similar between translocated and resident bobwhites. Jones (1999) concluded the limiting factor of the technique for large-scale restoration was the high cost of trapping bobwhites in Tennessee.

Ohio, public land, initiated in 1998. Wiley and Stricker (2017) report in detail on the history of Ohio Department of Natural Resources (ODNR) efforts in this proceedings. ODNR initiated a long-term statewide translocation effort to expedite population growth following population losses during severe winter weather. After years of poor success with release of first-generation progeny (F1), during 1998-2000 and 2005-2007, ODNR translocated 980 wild bobwhites from Kansas to five Ohio wildlife areas, and translocated wild bobwhite from Ohio sources. Based on population surveys during 1998—2012, Wiley and Stricker (2017) concluded populations had not increased.

Texas, Post Oak Savannah ecological region, initiated in 2004. Scott et al. (2013), collaborating with Texas Department of Parks and Wildlife, translocated 550 bobwhites to 2 sites during 2004–2006. Radio-tagged, translocated bobwhites had lower survival, nesting rates, and relative abundance, compared to residents. Scott et al. (2013) speculated that restoring bobwhite populations in fragmented landscapes with few remaining bobwhites might be impractical.

In addition to these published accounts of PRT, the NBCI Translocation Survey revealed unpublished translocation between state wildlife agencies since 1980. For example, Maryland provided bobwhites to Pennsylvania, Illinois twice provided bobwhites to New Jersey, Texas provided bobwhites to unidentified states, and Kansas provided bobwhites to Colorado. Colorado Parks and Wildlife currently recognizes establishment of these bobwhites near Trinidad, Colorado (accessed 20 February 2017). Moreover, unpublished translocation exchanges among private landowners to supplement hunting have occurred in the past. Whether the translocation was public or private, the motivation was often to provide increased hunting opportunity because of population growth from translocated bobwhites.

In summary, many of the state agency translocations were undertaken along the northern part of the species' range to remedy local population declines, in some cases local extirpation, caused by severe winter weather. A common catalyst for translocation was recreation, hunting or field trials, with state agencies being responsive to requests from hunting organizations and their concern about population declines, or lack of hunting opportunity. The effect of reintroduction and restocking on population abundance was in general neutral. Short-term site fidelity and reproduction were common, but long-term increases in bobwhite populations were lacking. In general, project study designs resulted in a substantial amount of uncertainty regarding efficacy of translocation. For example, control sites lacking any bobwhites were uncommon, and post-translocation bobwhite lineage was not traced to translocated bobwhites. The reason for low population sizes, even with sufficient habitat, likely determines the probability of translocation success.

REASONS FOR TRANSLOCATION

Biological and Ecological Reasons

Overcoming small population sizes. Remnant, isolated populations of bobwhites may not have the capacity to rebound even after the extrinsic factors causing their decline (e.g. severe winter weather, drought, etc. [Errington 1933, Roseberry 1962, 1989]) are no longer present. A demographic Allee effect, or positive density dependence, occurs when population vital rates decrease as a result of abundances below a minimum threshold and can manifest through a variety of processes (Deredec and Courchamp 2007, Armstrong and Wittmer 2011). Allee effects may influence bobwhite populations through several likely mechanisms. Decreased probability of locating a reproductive partner is the most commonly recognized mechanism causing Allee effects across all species (Deredec and Courchamp 2007) and may have implications for bobwhite reproduction if low densities preclude pair formation. Social prey species tend to be more vulnerable to predation at lower densities leading to lower survival (Gascoigne and Lipcius 2004, Armstrong and Wittmer 2011). Williams et al. (2003) identified optimal covey size in bobwhites to be approximately 11 birds. They observed lower survival, decreased group persistence rates, and higher movements for covey sizes below the optimal size (Williams et al. 2003). Additionally, bobwhite populations are known to exhibit large annual fluctuations (Lusk et al. 2007). Even weak Allee effects could have substantial impacts on populations where there is a large degree of stochasticity in annual vital rates (Dennis et al. 2016). Restocking wild bobwhites may eliminate the negative effects of low density if the number of individuals added to the population brings the total population above the minimum threshold (Guthery et al. 2000).

Issues of connectivity. Although bobwhites are generally recognized as the least mobile of gallinaceous bird species, dispersal can still play an important role in population dynamics through a rescue effect, the process where populations at low density are augmented by individuals from populations with higher densities (Brown and Kodric-Brown 1977, Townsend et al. 2003). Habitat fragmentation has long been recognized as the main driver of range-wide bobwhite declines (Hernández et al. 2013), and inhibits natural recolonization or augmentation of depleted populations by decreasing dispersal (Houde et al. 2015). When habitat fragmentation is high, the cost of dispersal (in terms of mortality) is also high because dispersers must traverse a matrix of unsuitable habitats (Terhune et al. 2010, Graves et al. 2014). Thus, natural recolonization rates may not be sufficient to restock isolated populations that have declined due to extrinsic factors such as winter weather or drought, or to re-establish populations following a habitat restoration. Restocking or reintroduction using translocation in this circumstance may serve as a viable tool for "artificial dispersal" or to enhance naturally occurring dispersal (Seddon 2010, Terhune et al. 2010, Houde et al. 2015). However, these fragmented populations are more susceptible to local extirpations; thus, translocations in these situations have a high probability of failure (Scott et al. 2013).

Perceptual Errors. Perceptual errors may present another limitation to bobwhite recolonization of restored habitats if cues are present that cause individuals to perceive the habitat as poor when in actuality it is good (Gilroy and Sutherland 2007). This may occur if there are anthropogenic cues or if the new habitat is sufficiently different from the source area habitat (Gilroy and Sutherland 2007). However, for social species such as bobwhites, the addition of conspecifics to the landscape may help to change those cues by signaling to dispersers that the habitat is suitable (Bayard and Elphick 2012, Andrews et al. 2015). Thus, the addition of bobwhites to a restored habitat where none currently exist may help to improve the colonization rates from naturally dispersing birds by improving the perception of habitat quality. However, translocated birds may also perceive habitat as inferior and disperse—leaving the site no better off before translocation.

Stakeholder-driven Motivations for Translocation

The desire to begin a wildlife translocation effort may be initiated by a private landowner, a non-governmental agency (NGOs), a government agency, or any number of stakeholders. A recent survey of authors of translocation efforts showed that most efforts were funded by federal (67%) and state governments (65%). Universities and local NGOs were cited as requesting or funding translocations at 53% and 34%, respectively (Brichieri-Colombi and Moehrenschlager 2016). All stakeholders must be well informed of the positives and potential negative effects of translocation efforts. Outside of biological obstacles to successful translocations, non-biological factors can also negatively influence programs. Public relation and education efforts can increase support by the public and governmental leaders (Reading et al. 1997). While state agencies operate under the Public Trust Doctrine to manage wildlife for the benefit of all people, the stakeholders served are an increasingly changing demographic. Manfredo et al. (2003) suggested that views toward wildlife have shifted from more utilitarian to protectionist. In this case, it may be difficult to convince stakeholders that it is necessary to increase populations of a species for the desired result of a huntable population. Other factors that may affect bobwhite population restoration efforts are the mandate to achieve quick results, financial, political agendas, and interest from the public as stakeholders. Bobwhite are a socio-economically important species. Bobwhites provide both consumptive and non-consumptive benefits with the former being the primary reason for their intentional management. However, the latter (non-consumptive) benefit is becoming more and more prominent in the face of precipitous range-wide decline, local and regional extirpations, and range contraction. For example, it is common vernacular of today for landowners to simply want to see or hear bobwhites again.

CONCERNS FOR TRANSLOCATION

Biological and Ecological Concerns

Genetic Implications of Translocations. Population restoration techniques should consider several factors prior to translocating animals in order to maximize reintroduction or restocking success and meet population goals. Because the translocation of wild animals can affect the genetic structure and make-up of species and populations, the genetic implications of translocation must be considered prior to translocation.

There are both genetic benefits and risks associated with PRT. Possible genetic benefits derived from translocation may include enhanced reproductive fitness, increased genetic variation, and improved adaptability of a population under environmental pressures (Weeks et al. 2011). Genetic risks of translocation include outbreeding depression (i.e., decreased reproductive fitness because distinct populations were attempted to be crossed), hybridization of related species, reduced genetic diversity, loss of historic genetic records, and the loss of a locally adapted population (Avise 2004, Weeks et al. 2011). Given the large number of genetic benefits and risks associated with translocation, it is important that managers weigh these genetic implications on a case-by-case basis prior to translocation. To assist managers in weighing these implications, Weeks et al. (2011) developed two tools (a decision tree and risk-assessment framework) to identify benefits and risks of translocation, assess and mitigate risks, and provide translocation guidance even when biological and genetic information for a species is lacking. We recommend managers use these tools when contemplating PRT as a management or conservation practice.

Fortunately, the bobwhite is an intensely studied species and thus information generally is available to guide translocation decisions. In the past, as many as 24 subspecies of northern bobwhite were described using male plumage and geographic distribution; however, currently 19–22 subspecies are acknowledged (Brennan et al. 2014, Madge and McGowan 2002, Williford et al. 2014, Williford et al. 2016). Recent mitochondrial DNA analysis found that the phylogeographic structure of bobwhites west of the Mississippi River was not consistent with the proposed subspecies distribution and more variation was found within populations than among populations (Williford et al. 2014). Therefore, it is suggested that many previously described bobwhite subspecies are not actually distinct taxonomic units (Williford et al. 2014); however, the Florida subspecies (*C. v. floridanus*) may be a distinct subspecies and likely should only be translocated within the peninsula of Florida (Eo et al. 2010).

The lack of genetic distinctness among subspecies is particularly surprising because physical differences such as plumage and patterns are apparent between subspecies (Williford et al. 2014). Even bobwhites in eastern and central United States that have more consistent plumage but vary in body size and colors (Williford et al. 2014). The physical variation (e.g. color, size, plumage pattern) between subspecies may be caused by adaptation to local or regional environments despite the fact that subspecies may not be genetically distinct populations (Williford et al. 2014). Thus, if bobwhites are locally adapted to their environment, then it is possible that bobwhite populations native to a region may be more fit to survive and reproduce in that region than bobwhites from a different region. For example, in the northern fringe of the bobwhite range where severe winter weather is common, size of bobwhites affects heat loss, and thus energy balance is an important factor to consider in the context of local environmental adaptation (reviewed by Burger et al. 2017, this volume). However, Hereford (2009), a comprehensive study of published research related to translocation, reported that the fitness costs associated with local adaptation are weak and not strong enough to prevent adaptation to multiple environments. This study did find that fitness costs associated with local adaptation were stronger when native environments differed greatly between populations and when a population adapted to an environment significantly different than its ancestor's environment.

Diseases. Numerous macro- and micro-parasites can cause morbidity and mortality in bobwhites. Among some of more common pathogens are protozoon coccidea, *Salmonella* sp. bacteria, and avian influenza viruses. These are thoroughly reviewed by Peterson (2007). Managers need to have concern for diseases for two key reasons of equal importance. When transferring bobwhite from source populations to new areas, managers must avoid moving diseases into new areas where existing populations of bobwhite and other bird species could be jeopardized. Likewise, managers should avoid translocating bobwhite into high disease risk areas that could jeopardize translocated bobwhites. For example, areas where there are large numbers of backyard and industrial poultry (Garber et al. 2007, Madsen et al. 2013).

The U. S. Department of Agriculture (USDA), and state veterinarian offices have regulatory authority over movement of birds. This authority includes both in-state as well as out-of-state movement. The USDA and state veterinarians are concerned with movement of diseases that may cause morbidity and mortality in domestic bird flocks such as commercial poultry. These entities require defined testing of birds for certain diseases of concern to agriculture. Often testing is based on the testing standards for the National Poultry Improvement Plan (USDA Veterinary Services 2014). State veterinarians may define additional disease tests before accepting birds into their jurisdiction from out of state or movement between different locations within a state.

Planning for a bobwhite translocation should include the following considerations:

1) Consultation with state veterinarian and USDA Veterinary Services;
2) Obtaining the services of a veterinarian to provide necessary health inspections and to oversee collection of samples; and,
3) Arrangement of a properly certified laboratory to conduct tests.

Wild bird supply. Historic efforts to translocate wild bobwhite have been profuse and widespread, with records dating back to the 1700s, and including destinations such as the West Indies, Peru, Hawaii, Europe, New Zealand, etc., and many U.S. states (Long 1981). Although comprehensive verified data on the quantity of bobwhites translocated is difficult to determine, records from Texas show 3 contracts over a 2-year period in the 1930s for 10,000-18,000 wild bobwhites each, from Mexico to Texas, and that costs were increasing because of "the growing scarcity of quail in northern Mexico…trapping operations which now must be carried on deeper in the interior of the country" (Texas Game, Fish and Oyster Commission 1939). New Jersey has a record in 1899 of receiving 30,000 wild bobwhites from Oklahoma (Chanda et al. 2011). Several state agency coordinators report similar translocations of bobwhites from Mexico. Similarly, between 1990 and the present, bobwhite research studies amassed sample sizes in the 10s of thousands (e.g., Burger et al. 1995, Sisson et al. 2009, Ruzicka et al. 2016). Thus, in the context of possible limitations to translocation, capturing wild bobwhites *per se* appears unlikely assuming some source populations remain.

Despite the relative ease of capturing bobwhites, the long-term, widespread decline in bobwhite populations in the late 20th Century resulted in decreased supply of birds for translocations. Both the Ohio Department of Natural Resources, in 1993 (Wiley and Stricker 2017), and the Canadian Ontario Ministry of Natural Resources, in 1994 (James and Cannings 2003), reported that insufficient numbers of wild bobwhite among states delayed or ended translocation projects. However, some private landowners in a few states (e.g., Texas, Georgia, and Florida) have historically been willing to allow trespassing on their property to translocate birds. However, the birds themselves belong to all residents of that state and the state wildlife agency is entrusted to decide whether or not to allow translocation.

Management Constraints

The Lacey Act. Understanding state and federal laws concerning bobwhite translocation is essential to success of PRTs. While most states have general statutes prohibiting capture and possession of native wildlife, specific regulations governing capture and transport for translocations are not developed for the majority of states in the bobwhite range. Without such state-specific regulations, the legality of capture and translocation of native birds falls directly under the Lacey Act. First passed in 1900 the Lacy Act prohibits, among other things, "*import, export, transport, sell, receive, acquire, or purchase any fish or wildlife or plant taken, possessed, transported, or sold in violation of any law, treaty, or regulation of the United States or in violation of any Indian tribal law*" (Lacey Act 1900). If capture and possession of native wildlife is prohibited, then importing or exporting those animals would be illegal under the Lacy Act due to the method they were taken. Therefore, capturing and translocating birds within or across state boundaries is prohibited under the Lacey Act in the absence of state-specific statutes that permit capture and transport of native wildlife for translocation. We recommend states interested in PRT investigate the opportunity for drafting specific legislation regarding translocation.

State Agency Willingness. In autumn 2016, NBCI surveyed quail coordinators of the 25 state wildlife agency members of the National Bobwhite Technical Committee for information on bobwhite translocation. Based on 18 responses, 44% of coordinators (8 states) indicate potential ("very-likely," "somewhat-likely," or "neutral") for their state agency to be a source of wild bobwhites for translocation to other state agencies during the next 5 years. Affirmative responses were contingent on several factors, including existence of a biologically based evaluation of recipient site, publication of a national translocation guidance, and a positive trend in the donor state's quail population. At the time of the survey, quail populations were very high in the majority of states willing to donate bobwhites. Only two state agency quail coordinators indicated their agency is "very likely" to be a source of bobwhites, Kansas Department of Wildlife, Parks and Tourism, and Georgia Department of Natural Resources. Kansas has a long history, since the 1980s, of donating bobwhites, providing birds to state agencies in Colorado, Indiana, and Ohio.

The Georgia Department of Natural Resources Wildlife Resources Division is increasingly facilitating exchange of wild bobwhites between private landowners under their 2006 Game Management Policy Statement: Q-1 Quail Translocation (Sisson et al. 2012). Donations of Georgia bobwhites to private entities in Maryland, New Jersey, North Carolina, and South Carolina necessitated approval by state agencies in those states, following the Public Trust Doctrine. Under the Public Trust Doctrine, state wildlife agencies have jurisdiction over resident wildlife including wild bobwhite with the responsibility of managing the species to benefit all the state's citizens (Decker et al. 2015). Peterson et al. (2016) point out that interpretation of the merits of species conservation via privatization (e.g., translocation managed by private entities) has been constantly evolving. Following the Public Trust Doctrine, some coordinators answering the NBCI survey emphasized that translocation of bobwhites out of their state must provide a clear benefit to the citizens and hunters of that state. For example, a common practice among state agencies has been to exchange species, e.g., wild turkeys for river otters (*Lontra canadensis*). For bobwhite conservation, several coordinators expressed the opinion that the private lands model has the potential to play a key role in bobwhite conservation if protective measures are in place and the spatial scale is large enough to increase the probability of long-term population viability. Private lands could be the foundation of a state's bobwhite recovery, augmenting management, research and translocation that may be cost prohibitive to state agencies. Private land owners can provide large-scale habitat management, exemplary land stewardship, and conservation advocacy benefiting a suite of species, both fauna and flora. Moreover, bobwhites are no longer a priority for some state agencies, partly a result of declining numbers of small game hunters, e.g., the number of small game hunters declined 49% from 1975-2000 (Flather et al. 2009).

BEST MANAGEMENT PRACTICES FOR TRANSLOCATION SUCCESS

The decision to use PRTs is driven by stakeholders and agencies wanting to meet conservation objectives (e.g., state agency quail and biodiversity plans) under constraints of policies and laws. If PRT is considered as a management action to achieve those objectives, the best science should be used to inform its use. It should be instituted on a site-by-site basis, and decisions governing its implementation should take into account knowledge of the species' life history and ecology. This approach would ideally increase the efficacy of PRT and help to guide its role in conservation planning and management. The success of PRT is conditional on several key factors including sufficient habitat, minimizing stress during translocation, using the right source population, the presence of conspecifics, timing of the translocation in the bobwhite annual cycle, and releasing enough birds (Table 1).

Sufficient habitat. Guthery et al. (2000) suggests that to avoid local extinctions in the face of summer and winter extreme events about 800 birds in autumn is needed with 800-1,600 ha of habitat. Sands et al. (2012) extended this work and indicated that a greater amount of habitat is needed to sustain spatially-structured bobwhite populations in the presence of harvest where as much as 9,600 ha of habitat is needed with a 40% harvest rate. Thus, we do not recommend exploitation of newly reintroduced or restocked populations until the population has stabilized ($\lambda = 1$) and 800 birds. Terhune et al. (2010) recommended properties should be large (>600 ha) and contiguous to increase site fidelity and survival post-release where population colonization is limited due to isolation from source populations. To date, translocation to smaller sites (<600 ha) has not experimentally been tested and, as such, we do not recommend doing so (Terhune et al. 2010). The minimum habitat requirements of the NBCI Coordinated Implementation Program (Morgan et al. 2016, sidebar #1) follows Guthery et al. (2000) and Terhune et al. (2010), but relaxes requirements for 100% contiguous sufficient habitat in space and time. The NBCI minimal criteria allow for conservation in the context of an abundance of insufficient habitat in a focal

Table 1. The critical steps to assure reintroduction or restocking success.

1. Determine if translocation is necessary and appropriate via an initial assessment of habitat and bobwhite abundance (Figure 2);
2. Identify source site for wild bobwhites; utilize the decision tree and risk-assessment framework for Weeks et al. (2011) to identify benefits and risks of translocation, assess and mitigate risks, and provide translocation guidance even when biological and genetic information for a species is lacking;
3. Secure appropriate state permits (from source and recipient state) and identify disease testing requirements (from recipient state) and possible disease threats;
4. Capture wild bobwhites during mid-March to early-April using baited funnel traps (see Stoddard 1931), minimizing stressors such as handling and heat stress;
5. Upon capture, work up birds and record data (sex, age, weight, leg-band number, conduct health screening as stipulated in trap and transfer permit (e.g., extracting blood samples, gular swabbing);
6. Place birds into transport boxes (with air holes) in groups of ~11 individuals while trying to keep birds intact with original social groups; assure that the boxes don't let in light;
7. Transport birds immediately to release (recipient) site;
8. Release birds using a "hard-release[1]", during the daylight within 24 hours (preferably within 18 hours) of capture on the release site; and,
9. Monitor the population for 10 years to determine success (Figure 1).

[1] We recommended not holding the birds in a captive setting for acclimation (Parker et al. 2012). But birds should be released into cover and perhaps allowed to emerge from the transport box at their own will.

area, either because the land is primarily used for agriculture, or, management of plant succession (fire, mechanical removal of vegetation, etc.) renders areas insufficient for bobwhites for much of any one year. At this time, we recommend the following the minimum habitat area criterion as stipulated in Terhune et al. (2010), but we encourage future research to evaluate the sensitivity of landscape context and minimum habitat amount required to sustain viable population thresholds submitted via Guthery et al. (2000). The habitat is a means to get to >800 birds, thus, the habitat needed to sustain that population size is the targeted habitat area. We offer Terhune et al. (2010) and Guthery et al. (2000) as a minimum and a best management target, respectively.

Limiting Stress. Physiological stress is inevitable when moving birds to a new environment. Stress has been implicated as a major factor affecting wildlife translocations; however, by identifying and mitigating stress the translocation process can be improved (Letty et al. 2000, Teixeira et al. 2007, Chipman et al. 2008, Dickens et al. 2009, 2010).

Stress responses in translocated birds can be categorized as acute (short-term stress) or chronic (continuous stress). Acute stress includes a physiological response of adrenaline that signals increases in heart rate and blood flow to aid in a quick escape from threats (Parker et al. 2012). For example, evasion from a predator encounter would be considered the result of an acute stress response, which is beneficial to birds as a survival adaptation (Romero 2004). Alternatively, bobwhites are not evolutionarily adapted to manage chronic stress which can alter their physiology and compromise reproduction, immune responses, and metabolism; ultimately leading to death (McEwen 1998, Romero et al. 2009, Dickens et al. 2010). For example, wild birds held for long periods in captivity elicit a chronic stress response resulting in high mortality often observed after release (Armstrong and Seddon 2008).

Ultimately, the resultant pathology of stress is a factor of environmental vulnerability. For example, a lowered immune system leads to death by microbes and viruses, an altered predator response leads to predation, and altered reproduction could lead to a quick extirpation of bobwhites. While the categories of stressors are acute and chronic, Parker et al. (2012) identified 3 scenarios that elicit a stress response in wild animals: (1) lack of control, (2) unpredictability, and (3) novelty; all of which are introduced in the translocation process (Dickens et al. 2009). Thus, one goal of bobwhite translocations should be to identify and avoid stressors associated with all phases of the process (capture, holding, transportation, and release).

For example, Terhune et al. (2010) covered traps to minimize capture stress in bobwhites, and made great efforts to release all birds in less than 24 hours from time of capture. Abbott et al. (2005) found that injecting captured bobwhites with vitamin E and selenium increased their survival when translocated. Maho et al. (1992) found that any human handling of birds induced a stress response and suggested minimizing handling and processing time. Weiss (1968) and Dickens et al. (2009) suggested that a quick transition from capture to transport is vital as birds encounter stress from a myriad of changes in temperature, crowding, humidity, noise, light, etc. Holding pens are not recommended as they reduce the bird's ability to behave in a natural manner and should be avoided (Gelling 2010). When releasing translocated bobwhites, bird should be kept in familiar groups and released in environments similar to the capture site (temperature, humidity, structure, and nutrition). Additionally, any celebration or observation of releases should be done in a manner that to minimize stress and maximize animal welfare.

Using the right source. Prior to translocation, careful consideration regarding the source for translocated birds is necessary. However, source populations are often described inconsistently. For example, source populations, defined as the population from which birds were captured for translocation differs, in an ecological context, from source populations defined as the populations around a translocation site that could move into translocated sites. This distinction is critical as both could influence translocation success in different ways. For this section, we will refer to the population from which birds were trapped and translocated from as the source population and populations around the translocation site as neighboring populations. Few studies have experimentally evaluated the effect of source populations. We can glean anecdotal information from the literature but more research directly investigating the effect of source populations is needed. Troy et al. (2013) found source population had no influence on translocated mountain quail (*Oreortyx pictus*). However, Terhune et al. (2006*a*, 2006*b*) and Liu et al. (2000) found source population was important to success. Multiple mechanisms can influence the impact of source populations. For example, if site conditions of the source area differ considerably from the translocation area, the mechanism affecting success could be localized adaptations to habitat, weather, predator communities, populations of competitors for food and space, and interactions thereof. Therefore, the source population itself is not the mechanism, rather the bird's response to disparity in site conditions. Depending on geography, the further the source population from the translocation area, the greater the probability of differing site-specific adaptations, and therefore the greater the probability of failure. For example, translocation efforts in East Texas found that birds translocated from South Texas had lower survival rates than birds from another region of East Texas (<15 km away) (Lui et al. 2000). Similarly, Parsons et al. (2000) found that birds translocated from South Texas to East Texas were "inefficient in their ability to successfully nest, hatch eggs, and fledge chicks into the population. However, Downey et al. (2017) found weak evidence for an effect of distance on survival of translocated birds.

Consideration of latitude, Bergmann's Rule (Bergman 1847) and thermoregulation would prevent illogical selection of source populations due to disparity between body size of bobwhites, which range from ca. 160 g toward the south and 200 g toward the north. *If* energy balance is a limiting factor for bobwhites toward the north, birds from the southern extreme of the bobwhite range are illogical candidates for source populations to birds being translocated to the northern periphery of the range (Burger et al. 2017, this volume). Translocated birds lacking the genetic framework to adapt to conditions outside of their evolutionary roadmap are unlikely to adapt to conditions of which they have never been exposed. When local populations are completely extirpated, reintroduction via translocation can introduce demographic and genetic bottlenecks (Jamieson et al. 2007). Gregory et al. (2012) argued that genetic diversity of the source population was the ultimate factor of success with Evermann's Rock Ptarmigan (*Lagopus, muta evermanni*). Bobwhite translocations in areas of extirpation will be increasingly susceptible to genetic bottlenecks. Therefore, understanding the genetic diversity of source populations is important for translocation success. Furthermore, the expansion of bobwhite habitat around areas of translocation will reduce the probabilities of genetic bottlenecks.

Presence of conspecifics. Successful restoration efforts via translocation should occur prior to populations levels vulnerable to extirpation from stochastic events (Baxter et al. 2008). Recent bobwhite translocations with a positive population response were conducted where populations existed (Terhune et al. 2006*a*, 2006*b*, 2010). In each of these scenarios, bobwhite populations at the translocation site were at low densities (<1 bird per 3 ha), but not extinct. Scott et al. (2013), however, attempted translocation to area of central Texas that had been extirpated and the closest neighboring populations was 95 km away. The resulting unsuccessful translocation may have been due to the limited number of conspecifics at the translocation site and the fragmentation of the landscape. The importance of conspecifics in bobwhite translocation cannot be overstated. For example, Jones et al. (1999) observed 95% integration of translocated bobwhites into resident coveys that likely increased success of translocation. The exact density at which bobwhite populations should respond positively to translocation is not known and is likely site specific. The range of densities at which bobwhite will respond positively to PRT is unknown, but likely larger than range at which they cannot respond to translocation. In other words, a threshold density, below which augmentation via translocation is ineffective likely exists. At such a threshold, the Allee effect could render translocation efforts ineffective.

Releasing enough birds. Whereas release of translocated birds in coveys (8-12 birds) prior to the breeding season has become standard protocol (Terhune et al. 2006*a*, 2006*b*, 2010, Scott et al. 2013, Downey et al. 2017), and optimal covey size in bobwhites has been found to be approximately 11 birds (Williams et al. 2003), the density of released birds needed to produce a measurable translocation success is not known. Currently, no studies report the number of released birds relative to the translocation study area or target area (i.e., release density). This metric could influence success rates and efficiency of translocation efforts. Release density should theoretically vary with habitat type, quality, patch size, degree of fragmentation, historic density, distance to neighboring populations, density of neighboring populations, and management goals. However, this factor has not been evaluated and therefore, remains an unknown source of variation in translocation programs.

Spatial and temporal aspects of translocations. One-time translocations are common in the literature (Jones 1999, Liu et al. 2000, Scott et al. 2013), and a couple multi-year examples of failure (Frawley 1999, Wiley and Stricker 2017, this volume) that lack detailed measurement of bobwhites or habitat. Current descriptions regarding the spatial extent of release locations are vague and inconsistent. For example, Terhune et al. (2010) released birds at random locations within a stratified sample scheme, whereas Scott et al. (2013) used a uniformly distributed grid approach. However, the distances between translocated coveys is not reported. Considering the role of conspecific attraction in bird behavior (Ward and Schlossber 2004, Ahlering et al. 2006), proximity of release groups relative to release density could influence translocation success.

Time of year. Given adequate habitat management and a valid source of wild bobwhites, translocating individuals 3–4 weeks prior to the breeding season (during March) to provide ample time to acclimate to their new surroundings, but not longer than 3–4 weeks prior to breeding season to reduce mortality is important to success (Terhune et al. 2006b, Terhune et al. 2010).

REDUCING UNCERTAINTY ABOUT TRANSLOCATION SUCCESS

Assessment and Monitoring

Understanding the limits of translocation as a population recovery tool is inextricably dependent on sufficient evaluation and monitoring under varying scenarios. The range of approaches varies considerably among the published literature but does provide a rough roadmap for future studies. However, many questions remain unanswered regarding various logistical considerations associated with both pre- and post-translocation. While protocols exist for methodology of capture, banding, and tracking translocated bobwhites, a lack of consensus exists regarding multiple factors associated with the release process and how to evaluate outcomes. Terhune et al. (2006*a*) identified three mechanisms that largely influence translocation success: the source of the birds, the timing (season) of translocation, and the habitat conditions at the translocation site. These guidelines have served bobwhite translocation research in that subsequent translocation research has addressed these mechanisms but to varying degrees. However, the highly variable outcomes of bobwhite translocation efforts in the last two decades (Jones 1999, Liu et al. 2000, Terhune et al. 2006*a*, 2006*b*, 2010, Scott et al. 2013, Downey et al. 2017, Wiley and Stricker 2017, this volume) indicate that additional mechanisms warrant investigation (e.g., soft- vs. hard-release strategies) while existing mechanisms require further discussion. Before translocation efforts begin, decisions regarding population monitoring, source of birds, timing of translocation, release density and frequency, and release site must be made. Careful evaluation and assessment of these factors will increase efficiency and future successes of translocation efforts. Once translocation has been conducted continued monitoring and of survival, movement, production, health, and genetic quality must be conducted to evaluate factors that influence success.

Population Monitoring. —Restoration can only be evaluated with systematic, scientifically-based monitoring. Measuring translocation requires sufficient estimates of abundance pre-and post-translocation. Even when populations are low prior to translocation, effort must be made to adequately assess population trend (increasing, decreasing, stable) and size. Multi-year monitoring is important pre-translocation to determine population trajectory and therefore, implement translocation prior to extirpation (Griffith et al. 1989, Downey et al. 2017). Pre-translocation monitoring will also provide baseline indices to evaluate the outcome and interpret the magnitude of response of translocation efforts. Fall covey-counts and whistling male counts will both provide beneficial data to aid in evaluating translocation outcomes. Fall covey counts will also provide data on known locations of remnant coveys that could inform future translocation sites to increase probability of conspecific interaction. In situations where the goal of translocation is to augment existing, suppressed populations, data on body condition, survival, and reproductive metrics will be useful for evaluating translocation outcome (success/failure), but also to assess additional adverse (e.g., disease) or beneficial (e.g., increase in clutch size, body weight, nesting effort, etc.) effects that cannot be captured with passive monitoring techniques (e.g., covey counts). Maintaining a sample of banded and telemetered birds will provide the opportunity to capture subtle changes in populations that traditional monitoring could overlook.

After translocation, intensive passive (e.g., covey counts) and active (e.g., radio telemetry) monitoring are required to fully assess the outcome of translocation. In addition to traditional metrics gained from radio telemetry (i.e., survival and reproductive measures) data on movement and emigration out of the target area are needed to understand how translocated birds respond to the new environment. Research on differences in survival, reproduction, and movement of translocated birds is highly variable (Liu et al. 2002, Terhune et al. 2006*a,b*, 2010, Downey et al. 2017). Movement out of the translocation area could be a function of both the distance travelled from the source population, poor habitat on the release site, lack of conspecifics, and/or the disparity in habitat conditions between source and translocation areas. Therefore, intensive monitoring is necessary to adequately assess birds' response to translocation. Continuation of whistling male and fall covey counts, after translocation will provide a comparison of pre- and post-translocation population indices that will aid in determining the magnitude of population response to translocation. Population monitoring should continue for a minimum of 10 years, following the NBCI Coordinated Implementation Program (Morgan et al. 2016), to determine the establishment and persistence of the population.

Future Research Directions

Translocation to judiciously restore and augment bobwhite populations can only achieve large-scale success if we continue to use sound science to inform decision making. Therefore, more research is needed to evaluate a range of issues regarding multiple steps in the translocation process. For example, research that explicitly and experimentally evaluates the influence of source populations on translocation success must be conducted with considerations for local adaptations to habitat types, environmental stressors, and predator communities. Similarly, the genetic consequences of source populations from translocations has yet to be investigated. Measures of survival and reproduction are sufficient to evaluate the short-term effects of translocation, but the long-term impacts on evolutionary consequences will need to be evaluated in the future (Gregory et al. 2012). Research to determine the population thresholds below which translocations can succeed will be vital to prioritizing a population or area's candidacy for translocation and optimizing resource allocation. The importance of implementing translocations while populations can numerically respond is crucial to the success of translocation as a restoration tool (Griffith et al. 1989). Research that experimentally investigates varying release densities relative to habitat type, quality, patch size, degree of fragmentation, historic density, distance to neighboring populations, density of neighboring populations, and management goals will allow managers to optimize translocation efforts across diverse landscapes. Similarly, temporal and spatial distribution of release sites relative to release density will facilitate strategic translocation efforts thereby minimizing cost and time. Collectively, these research areas will add to the existing literature and provide a guiding framework for future translocation efforts.

Regardless of much needed further research, the implementation of reintroduction and restocking in the future fundamentally boils down to the question of these techniques causing population recovery. Said another way, would the population have recovered without the use of translocation? Translocation may not be the most effective use of limited resources (considering birds have some intrinsic value). In either case, sound experimental design is needed to continue to refine reintroduction science. Learning comes at a cost because more sites and control sites will be needed—these are sites that restoration could have occurred on if learning was not an objective. We operate under the assumption that sites for population restoration cannot be identified at random because of the limited number of landscapes suitable for restoration. Thus, a Before-After-Control-Impact (BACI) design is likely the most feasible design to determine causality. The control sites should be areas with sufficient habitat (>800 ha) that do not receive translocated birds. The treated sites should have sufficient habitat and receive translocated birds. Sufficient habitat can be measured using the Coordinated Implementation Plan Habitat Assessment (Morgan et al. 2016). Treatment and control sites should be replicated. The number of replicates will depend on the site-to-site variability and the effect size. The effect size (increase in population as a result of the treatment) could be large, if it exists, making the number of replicates needed relatively small. We recommend monitoring annually for 10 years post-translocation to evaluate long-term success (Figure 1) following the Coordinated Implementation Plan's monitoring protocol (Morgan et al. 2016). We strongly urge those interested in future translocation efforts to collaborate with scientists on design and implementation to optimize success while sufficiently monitoring and documenting for continued learning.

SUMMARY AND CONCLUSIONS

Bobwhite conservationists need to know what tools are effective at meeting population objectives. Population restoration techniques—restocking and reintroduction—even after multiple decades of research have a cloud of uncertainy around them making definitive conclusions difficult. Unfortunately, this uncertainty is mostly due to experimental designs that do not allow for isolating the cause of failures or successes. In the examples of failure, habitat was likely not sufficient or at the least the area was insufficient to support a growing population of birds thus creating the "pouring down the sink phenomenon (sensu Pulliam 1988)" (Seddon 2010); however, it can't be ruled out that the translocation itself failed. The successful examples illustrate that translocated birds' survival and reproduction is comparable to their resident counterparts. However, it does not permit a definitive conclusion that translocation was the cause for population response given experimental controls were lacking in most studies to date (excluding Terhune 2008, a restocking experiment). Nonetheless, these successes provide enough evidence for the benefits of translocation that warrants the continued practice and exploration of restocking populations in areas of sufficient habitat to meet population goals but under certain criteria (Figure 1). The sufficient habitat criteria should be applied as a stringent criteria for potential PRT projects and any deviation from this criteria should be treated as experimental and done so under the guise of research not management. Even under this criteria the success of PRT is not guaranteed considering our current uncertainty regarding knowledge of bobwhite habitat and other looming factors contributing to population declines. Furthermore, even populations of respectable size (>800 birds) in sufficient habitat are subject to local exinction due to environmental stochasticity which is exacerbated in fragmented landscapes (Anderson et al. 2017). Potential reintroduction projects, in particular, should consider the quantity of birds translocated. Assuming habitat is sufficient and a low density population, immigration of other wild bobwhites into the site is limited, making any rescue effect unlikely; therefore, the translocation itself must get the population over any critical population threshold (i.e., 800 birds). Uncustomarily, again assuming habitat is sufficient and population goals have not been met, a plausible approach is to wait a few years to see if the population responds without PRT (Figure 2). However, this "wait and see" approach is not without risk. For example, if a small population exists in sufficient habitat, waiting a few years could allow the population to continue to decline with possible local extinction. An inherent, often forgotten risk in PRT projects, is the consequences to the donor site, thus, any removal of birds from donor sites should be treated similar to harvest and the minimim bird criteria (800 birds) should be applied to donor sites too—don't rob Peter to pay Paul.

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		Habitat Sufficient	
		Yes	No
Wild Birds Present	Yes	Restocking through translocation or wait longer.	Manage habitat
	No	Reintroduction through translocation or wait longer.	Manage habitat

Fig. 2. Conceptual decision matrix for determining what type of translocation effort should be implemented (restocking or reintroduction) and if it should be implemented conditional on the amount of habitat. The decision assumes that the population is below the target for the entity; otherwise, continued management under the status quo is warranted.

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A FOCUSED HABITAT APPROACH FOR NORTHERN BOBWHITE RESTORATION IN KENTUCKY

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ABSTRACT

The Kentucky Department of Fish and Wildlife Resources has measured northern bobwhite (*Colinus virginianus*) population trends since 1960. During that span, northern bobwhite steadily declined because clean agriculture, fescue-sod, plant succession, and development eroded habitat suitability. Multiple efforts have failed with regard to restoring northern bobwhite numbers. Over 3.5 million northern bobwhite were released by the Department over a three decade period. Habitat efforts on private lands were deployed for over 20 years with mixed results. Support for the habitat restoration efforts waned. In 2008, the Department unveiled a new strategy centered on restoring concentrated habitat in focal areas. From 2008 to 2013, the Department managed habitat and monitored breeding northern bobwhite on 5 focal areas that were distributed throughout the state. Focal areas ranged in size from 1,155 to 16,517 ha. A total of 109 breeding bird survey points were monitored annually with up to three repetitions. Habitat management activity was also tracked. We used distance sampling to model density-dependent and density-independent population growth. Across the study, there was a 0.992 probability that our populations were growing with a mean region-wide, density independent growth rate of 35.7% annually. We were able to grow populations in an array of landscapes that were dominated by agriculture and grasslands. Management actions maintaining $\geq$10% of the focus areas in early successional habitat consistently supported growing northern bobwhite populations. The unique nature of our focal areas made them poor laboratories for field study, so future multi-state collaboration may be essential to understand the factors driving northern bobwhite growth. A better understanding of northern bobwhite population growth as it relates to landscape, management, weather, and harvest metrics will improve management prescriptions for northern bobwhite habitat on larger landscapes in the future.

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Key words: *Colinus virginianus*, habitat, Kentucky, northern bobwhite, restoration

The first recorded declines of northern bobwhite (*Colinus virginianus*) in Kentucky were reported in 1917 (Kentucky Game and Fish Commission 1975). Harsh winters and eroding habitat conditions reduced populations to levels that motivated the first attempts at restocking. By 1930, roughly 100,000 northern bobwhite were translocated from Mexico. In 1932, translocation efforts were suspended and replaced by captive propagation efforts (Kentucky Game and Fish Commission 1975) that continued through 1989. Over that time span, an estimated 3.5 million northern bobwhite were released (Morgan and Robinson 2008). Pen-reared northern bobwhite release has repeatedly failed toward restoring populations throughout the last half century (Barbour 1950, Roseberry et al. 1987, Perez et al. 2002, Thackston et al. 2012).

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Despite the substantial efforts to mitigate waning northern bobwhite numbers in Kentucky, the population continued to decline. Breeding bird and rural mail carrier surveys in Kentucky demonstrated steady declines from 1960 to present with an annual rate of decline of 3% (Sauer et al. 2014, Morgan and Robinson 2015). Kentucky was joined by the majority of states across the northern bobwhite range with an annual range-wide decline rate of 4% from 1966 to 2012 (Sauer et al. 2014).

The focus on pen-reared release and captive propagation treated the symptom of widespread declines, not the cause. Clean agriculture, fescue-sod, plant succession, and development transformed Kentucky's landscape; the loss of widespread, connected habitat has been repeatedly identified as the root cause of the northern bobwhite decline (Brennan 1991, Guthery 1997, Burger 2002, Veech 2006, NBTC 2011). The Kentucky Department of Fish and Wildlife Resources (KDFWR) embraced that theme in 1986 with the establishment of one of the nation's first, state-funded habitat programs, the Habitat Improvement Program (HIP). During its inaugural 2 years, the program provided technical guidance to private landowners aimed at habitat improvement for declining small game populations (i.e., northern bobwhite, *Bonasa umbellus*, *Sylvilagus floridanus*). In 1989, HIP was funded with a $90,000 cost-share budget capped at $500 per landowner. Kentucky had charted a new course for recovering northern bobwhite.

Over the next 20 years, private lands biologists opportunistically worked with private landowners that invited them to their property (a reactive approach). HIP, US Forest Service (Forest Stewardship), and US Department of Agriculture (Farm Bill) conservation funding sources were deployed to cost-share enhancements. This conservation delivery strategy fostered widespread and piecemeal habitat enhancements, because Kentucky is over 90% private ownership (Wethington et al. 2003) with a 66 ha average farm size (U.S. Department of Commerce 2009). Field biologists anecdotally reported farm-based northern bobwhite responses to habitat management; however, state-wide survey data still demonstrated the continued declines. As the year's progressed, anecdotal reports curbed and sportsmen questioned that habitat was the primary problem.

The 21st Century brought new thinking to northern bobwhite conservation. The Bobwhite Quail Initiative (BQI) (Thackston et al. 2006) and the Coordinated Upland habitat Restoration and Enhancement Program (CURE) (Howell et al. 2002) were novel northern bobwhite programs established in Georgia and North Carolina, respectively. Both programs focused habitat efforts at multi-county levels with additional manpower and funding. They also monitored bird response and landowner attitudes. The programs were demonstrating positive northern bobwhite responses on many areas and informed agencies how to modify activities in circumstances where northern bobwhite did not respond (Thackston et al. 2006, Mark Jones, personal communication).

Soon after, the Northern Bobwhite Conservation Initiative (NBCI) (Dimmick et al. 2002) was released. A national vision for northern bobwhite restoration was established for 22 states. The goals for habitat and birds were defined at the Bird Conservation Region (BCR) level, and states were challenged to "step-down" those goals through state-based initiatives. The Missouri Department of Conservation (MDC) was the first state to create a strategic approach to deliver the NBCI to the ground and established county-based habitat targets (Missouri Department of Conservation 2003).

The culmination of a range-wide plan and state-based northern bobwhite restoration activity prompted KDFWR to aggressively pursue its own initiative. Contrary to MDC, we took a different approach for stepping down the NBCI in Kentucky. We lacked the manpower and funding to reasonably deliver state-wide conservation on the ground, and most notably, we lacked the knowledge of northern bobwhite response to habitat management at multiple scales (i.e., farm, focus area, and landscape) to confidently subdivide habitat targets across counties. Therefore, we created a strategic plan (a proactive approach) centered upon proving northern bobwhite could be restored at the focus area level (sub-county) with targeted habitat restoration and maintenance (Morgan and Robinson 2008). Herein, we present the results of focus area monitoring from 5 Kentucky focus areas from 2008 to 2013.

STUDY AREA

Five areas were identified as focal area projects within Kentucky. The focal areas had variable sizes, land cover compositions, and landscape contexts (Table 1). All were located between 37°-38° N latitude and 84°-89° W longitude (Figure 1). Climate is Humid Subtropical characterized by relatively long, hot summers and short, mild winters with brief episodes of severe cold. Four of the areas (Shaker Village, Bluegrass Army Depot, Hart County CREP, and Livingston County) are within the Interior Plateau Level III ecoregion. Gently rolling hills with some areas of steep relief, karst topography, and deeply entrenched rivers are typical landforms for the Interior Plateau in Kentucky (Woods et. al. 2002). Peabody WMA falls in the Interior River Valleys and Hills Level III ecoregion. Uplands of moderate relief dissected by wide, poorly drained stream valleys are typical of this ecoregion (McDowell 1986). There is a long history of coal extraction including surface mining in this region. Forests in our study were typified by mature, closed canopy oak (*Quercus* spp.) and hickory (*Carya* spp.) with little understory vegetation and assumed to be poor northern bobwhite habitat. Peabody WMA forests were the exception, because eastern cottonwood (*Populus deltoides*), green ash (*Fraxinus pennsylvanica*), and red maple (*Acer rubrum*) dominated overstories were open-canopied with developed understories (Brooke et al. 2015). Despite the enhanced value to northern bobwhite, they did not represent breeding habitat.

Focus areas were selected based on several criteria. The coarse aim was a mix of private and public land focal areas well distributed across the state. Finer selection

Table 1. The size (ha), ownership, and land cover composition (%) of northern bobwhite focus areas and surrounding landscapes (3000-m buffered area) in Kentucky from 2008-2013.

			Developed		Forest		Open		Water	
Area	Size	Owner	Focus	Landscape	Focus	Landscape	Focus	Landscape	Focus	Landscape
Blue Grass Army Depot	5,875	Public	3.6	8.3	47.0	14.8	48.3	76.3	1.1	0.6
Hart County	8,024	Private	0.1	0.1	14.6	21.9	85.2	77.7	0.2	0.3
Livingston County	16,517	Mixed	0.0	0.6	46.6	36.1	47.3	42.7	6.0	20.5
Peabody WMA	8,847	Public	0.5	1.7	52.9	43.1	35.3	47.0	11.2	8.1
Shaker Village	1,160	Private	0.0	0.6	35.3	37.8	64.5	59.2	0.2	2.4

criteria included: existing northern bobwhite populations (based on KDFWR staff knowledge), specialized manpower, land use type, opportunity for management, area size, and landowner/manager interest. Efforts were also made to avoid, to the extent possible, areas that had a history of pen-reared northern bobwhite release. Landscape context was considered through comparisons to Kentucky's county prioritization model (Morgan and Robinson 2008, Morgan et al. 2012).

METHODS

Habitat and Harvest Management

Wildlife biologists leading focal area management activities strived to maximize annual disturbance. The activities were centered on open lands management. Disturbance rotations were targeted for a 2-year return interval, but those goals were not always met. Weather was the largest contributor to mis-timed return intervals. Primary management practices included prescribed burning, disking, herbicide applications (targeting invasive species primarily), and plantings (native grass establishment and rotational food plots). Total and unique management acres were tracked annually from 2009-13 for each focal area (Table 2). Management activities were spatially noted across the study period, but they were not collected annually. Activities were ongoing prior to the project, but management intensity and scale was dramatically increased beginning in 2009. Hart County was the exception with massive habitat establishment in 2007 and 2008.

Hunting was controlled to the extent possible within the focus areas. Peabody WMA was changed from a statewide hunting season framework (approximately 92 days in west zone) with unlimited numbers of hunters to highly controlled quota hunts with 6 hunting days and 6 parties (maximum of 3 hunters per party) per day. Bluegrass Army Depot was closed to northern bobwhite hunting throughout the study. Livingston County and Shaker Village Focus Areas, were each hunted at conservative levels through guidance provided by KDFWR biologists. No specific hunting data was collected, but annual personal communications were

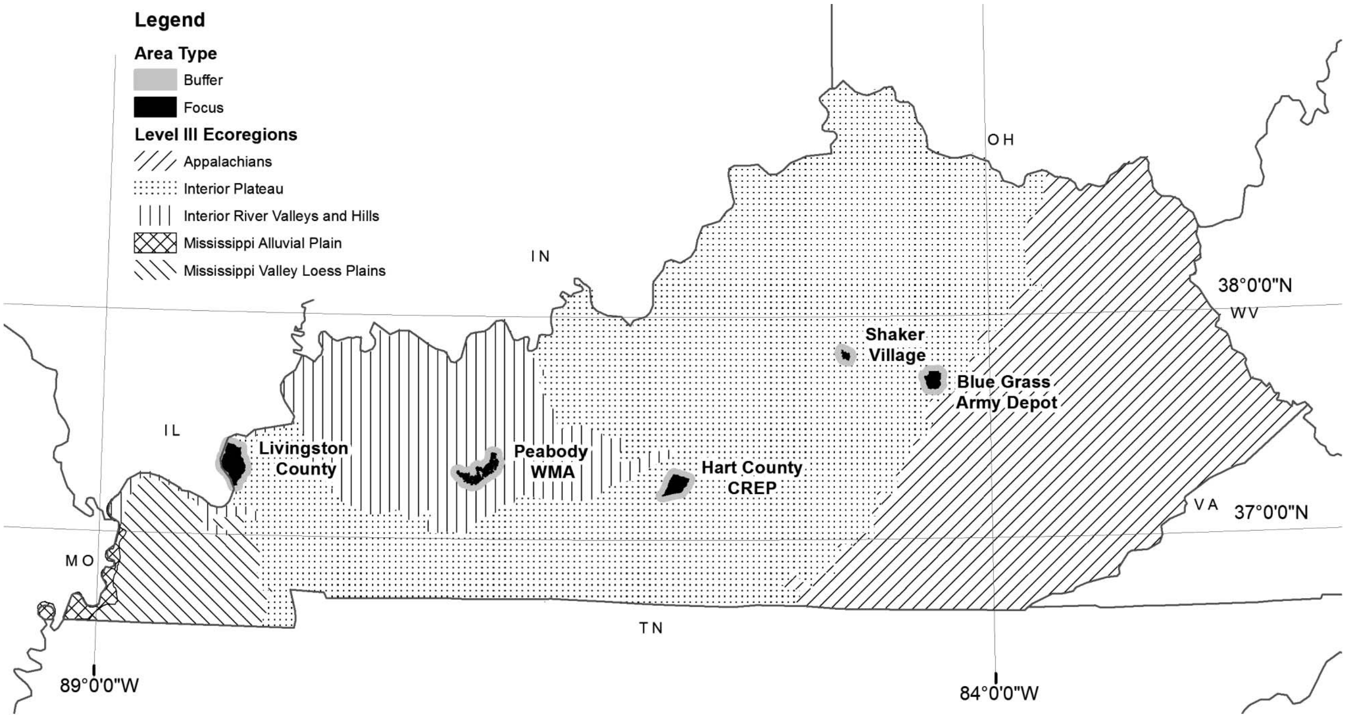

Fig. 1. The location, landscape buffer (3,000 m), and ecoregion of five, northern bobwhite focus areas in Kentucky, 2008-13.

Table 2. The total management practices implemented (ha) in northern bobwhite focus areas in Kentucky, 2009-2013.

	Focus Area				
Practices	Blue Grass Army Depot	Hart County	Livingston County	Peabody WMA	Shaker Village
Controlled Burning	1,554	0	1,399	729	547
Disking	6	87	63	450	0
Herbicide Application	95	140	372	160	576
Planting[a]	85	1,203[b]	616	45	227
Grazing	1,119	0	0	0	0
Woody Control	15	0	834	0	0
Total Unique Units[c]	531 (9)	1,203 (15)	1,660 (10)	845 (10)	418 (36)

[a] Includes planting of prairie restoration, fire break cover crops, and rotational, annual grain food plots.

[b] Practices completed in 2007 and 2008.

[c] Management practices were often repeated on the same hectare within a year and across years. The total eliminates double counting of hectares within and across years. Parenthesis represent proportion (%) of the focus area managed across the study period.

maintained. The Hart County Focus Area was available to state-wide hunting seasons (90 days in east zone) with no specific guidance from KDFWR biologists on hunt pressure.

Bird Monitoring

Bird monitoring was designed to measure northern bobwhite density across the focus area. We assumed northern bobwhite could be detected out to 500 m (Wellendorf and Palmer 2005), so we developed a 2000-m grid system for the entire state with ArcGIS. Two thousand meter grid cells provided a 500-m buffer around each point to maximize spatially independent monitoring points in each focal area. National Land Cover Data (NLCD, Fry et al. 2011) was reclassified into four classifications: open, forest, water, and developed to identify potential northern bobwhite habitat (hereafter, referred to as "open"). Each polygon was set to a minimum of 10 ha in size, because it was assumed the patch would represent the minimum suitable size a whistling male northern bobwhite would utilize.

Using ArcGIS, the statewide grid system was intersected with the focus area boundaries. A centroid point was placed in each grid cell as the initial starting point for a systematically random point selection process. Centroids located outside the focus area boundary were excluded from sampling. A single analyst at a 1:10,000 extent examined the national landcover dataset with respect to each centroid. Point selection started at the northernmost cell and systematically moved southward by rows.

We used the landcover dataset and Farm Services Agency (FSA, U.S. Department of Agriculture 2010) aerial imagery to conduct the point selection process. Transparency was set at 80% for the landcover dataset to allow simultaneous viewing of imagery to verify model accuracy when selecting points. Model misclassifications were corrected during the point selection process. For example, if a forest land cover was classified as "open" in the NLCD, but the imagery clearly showed forest, then observers interpreted it as "forest". The FSA aerial imagery was assumed to be 100% accurate.

The goal of point selection was to place the sampling point in the perceived center of the first open patch (bobwhite breeding habitat) within the 2000-m grid cell. If the centroid was in an open patch, the observer selected a point in the perceived center of that open patch within that 2,000 m grid cell. If the centroid was not in an open patch, then the observer looked due north and moved clockwise until intersecting an open patch. Should two independent patches (i.e., not connected as some point within the 2,000 m grid cell) exist along the same bearing, then the closest patch to the centroid was selected. Again, the observer placed the sampling point within the perceived center of the open polygon with respect to the 2,000 m grid cell. If no open polygons were intersected, then the point was placed in the perceived center of the patch identified by the centroid.

Standard breeding bird point counts were used by a single observer over a 5 minute monitoring period. Observers recorded calling locations of northern bobwhite and a suite of grassland songbirds on paper datasheets containing aerial images with superimposed distance bands (50,100, 250, and 500 m). Two aerial images were on utilized on each datasheet. A zoomed 100 m image (1:1,500 scale) was adjacent to a map encompassing the 500 m sampling area. Observers recorded birds that were within a 100 m on the zoomed map and birds beyond 100 m were recorded on the full extent map (1:6,000 scale). Time of first detection was noted next to the appropriate American Ornithological Union species code. Bird movements were tracked by the use of arrows on the datasheet during the sample period. If multiple observers supported a focus area, their sample points were spatially distributed across the area. The same observers were used across the study period. Up to three repetitions were completed each year (first 2 weeks of June, second 2 weeks of June, and first 2 weeks of July). Monitoring routes were reversed between repetitions.

Landscape and Weather Metrics

We used ArcGIS to assess landscape composition within and outside each focal area. The landscape was defined as a 3,000 m buffer around the focal area boundary (Twedt et al. 2007). NLCD 2011 values were reclassified to forest, open, water, and development land cover types and tabulated as a percentage within focus areas and the surrounding buffers. We used spatially-explicit shape file data from FSA to assess Conservation Reserve Program (CRP) contract acres for each year of the study. Those acres were also converted to a percent at the focus area and surrounding landscape. For assessing the variability among focal areas, we digitized management units across focal areas to calculate mean and standard deviation of compactness (a measure of shape in relation to edge), size of management units, number of management units, and average distance between management units (m).

We compiled summer breeding season and late winter weather data. We independently summed (no breeding season had positive and negative scores in a single season) positive and negative weekly Palmer Drought Index scores (National Oceanic and Aeronautical Administration 2016) from June through August to establish a wet and drought breeding season metric, respectively. For late winter weather, we used the closest weather station and counted the number of days below -5 degrees Celsius (Robel and Kemp 1997) in a calendar month from December through February each year.

Statistical Analyses

We used a model with two main components to estimate northern bobwhite population parameters: 1) a hierarchical distance sampling model to estimate detection probabilities and densities of northern bobwhite (Royle et al. 2004, Sollmann et al. 2015), and 2) a growth model to estimate density-independent and density–dependent population growth (Dail and Madsen 2011, Hostetler and Chandler 2015, Ricker 1954). We estimated three population parameters: abundance in the initial year of sampling (α), density-independent growth rate (θ_0), and regulation of growth rate by population density (θ_1). We modeled focus-area-level estimates for α and θ_0 as random variables drawn from a hierarchical (i.e., region-wide) distribution. The hierarchical distribution described what we could expect initial abundance and density-independent growth to be if other focus areas were established in our study region, thus broadening our inference. We used a negative binomial distribution to account for dispersion of counts in the initial year of sampling for each sampling location *i*:

$$\mathrm{N}_{\mathrm{i},1} \sim \text{Negative Binomial}(P, r)$$

$$P = r \big/ \left(r + \exp(\alpha\left[\mathrm{focus}_f\right]) \right)$$

$$\alpha\left[\mathrm{focus}_f\right] \sim \mathrm{Normal}(\mu_\alpha, \sigma_\alpha)$$

where P describes the number of successes (i.e., abundance), r describes dispersion, and $\alpha[\mathrm{focus}_f]$ describes expected abundance on the log scale differing by focus area f which were random draws from a normal distribution with mean μ_α and variance σ_α.

We used a Poisson distribution to describe abundance in subsequent years t=[2…6]:

$$\mathrm{N}_{\mathrm{i,t}} \sim \mathrm{Poisson}\left(\mathrm{N}_{\mathrm{i,t-1}} \cdot \exp(\theta_0\left[\mathrm{focus}_f\right] + \theta_1 \mathrm{N}_{\mathrm{i,t-1}}) \right)$$

$$\theta_0\left[\mathrm{focus}_f\right] \sim \mathrm{Normal}(\mu_{\theta 0}, \sigma_{\theta 0})$$

where $\mathrm{N}_{\mathrm{i,t}}$ describes abundance at site *i* for year *t*, $\theta_0[\mathrm{focus}_f]$ describes density-independent growth at each focus area which were random draws from a normal distribution with mean $\mu_{\theta 0}$ and variance $\sigma_{\theta 0}$, and θ_1 describes the strength of regulation of growth by population density. Regulation of growth by population density was assumed to be constant among focus areas.

We modeled observations (y) as a two-stage process. We estimated detection probability p using distance sampling information. Frequencies of observations in each of our distance classes were modeled as a multinomial process:

$$ty_i, \mathrm{t} \sim \mathrm{Binomial}(\mathrm{N}_{\mathrm{i,t}}, pCirc_{\mathrm{t}})$$

$$ydet_{\mathrm{i,1:nB,t}} \sim \mathrm{Multinomial}(y_i, \mathrm{t}, pi_{\mathrm{1:nB,t}})$$

where $y_{i,\mathrm{t}}$ describes the number of males detected for site *i* in year *t*, *pCirc* is the overall detection probability within a point count in year *t, ydet* describes the number of birds observed in each of our 5 distance bins (nB) at each site each year, and *pi* describes normalized detection rate for each distance bin.

For each distance bin *b* we modeled detection *p* as a half-normal function with a tuning parameter σ that varied by year:

$$p_{b,t} = \frac{\left(\sigma_t^2 \frac{1 - \exp(-db[b+1]^2)}{2\sigma_t^2} \right) \times \left(\sigma_t^2 \frac{1 - \exp(-db[b]^2)}{2\sigma_t^2} \right) \times 2\pi}{pa \times pix[b]}$$

$$pi_{b,t} = p_{b,t} \times pix[b]$$

where *db* is the boundary of each distance bin, *pa* is the area of a point count, and *pix* is the proportion of the sampling point area encompassed by each distance band. We then calculated *pCirc* as $\Sigma pi_{1:nB,\mathrm{t}}$. We analyzed the model in a Bayesian framework using three independent Markov Chain Monte Carlo (MCMC) simulations. We adapted the MCMC algorithm for 1,000 iterations then ran the model for 100,000 iterations and used visual interpretation of trace plots to determine model convergence. We calculated Pearson's residuals for each estimate of N in each year to determine model fit. We summarized results after discarding the adaptive phase and 50,000 iterations per chain.

The sample size of focus areas (n=5) and scale of information (i.e., focus-area-specific information only) precluded the inclusion of covariates in modeling efforts, so we conducted a Principal Components Analysis (PCA) as an informal way to evaluate variation of local, landscape (3,000 m), and weather variables among northern bobwhite focus areas (Table 3; PRIMER 5.2.9; Primer-E Ltd, Roborough, Plymouth, United Kingdom).

Table 3. Description of focus area variables included in Principle Components Analysis (PCA) of northern bobwhite focus areas in Kentucky, 2008-2013.

Variable	Description
year	year of data collection
size	focus area size (ha)
perforfoc	% forest composition within focus area
perforlan	% forest composition in landscape around focus area
peropnfoc	% open composition within focus area
peropnlan	% open composition in landscape around focus area
perwatfoc	% water composition within focus area
perwatlan	% water composition in landscape around focus area
perdevfoc	% developed composition within focus area
perdevlan	% developed composition in landscape around focus area
percrpfoc	% CRP composition within focus area
percrplan	% CRP composition in landscape around focus area
wet	sum of + weekly Palmer Drought Index scores(breeding[a])
drought	sum of – weekly Palmer Drought Index scores (breeding[a])
winter	count of days $\leq$ -5° C (December – January)
perinmgt	% of unique acres managed within focus area
fields	# of management unit within focus area
meanmgt	mean hectares of management units within focus area
meancom	mean compaction of management units within focus area
sdcom	SD compaction of management units within focus area
distmgt	mean distance (m) between management units

[a] Breeding season was June through August.

RESULTS

We sampled 40, 104, 104, 113, 106, and 63 sites from 2008 to 2013 and detected 0.450, 1.115, 1.202, 1.646, 1.415, and 1.825 singing male northern bobwhite per point, respectively. Detection probabilities from 2008 to 2013 were 0.124 (0.086—0.173 95% Bayesian Credible Intervals [BCI]), 0.238 (0.201—0.280 95% BCI), 0.249 (0.214 —0.286 95% BCI), 0.265 (0.230 —0.305 95% BCI), 0.253 (0.216—0.294 95% BCI), and 0.301 (0.247—0.365 95% BCI), respectively.

Our model predicted hierarchical mean density in 2008 to be approximately 16.5 ha/singing male (10.1—30.6 95% BCI) ($\mu_\alpha = 1.301$, 0.731— 1.837 95% BCI; $\sigma_\alpha = 0.440$, 0.058—1.358 95% BCI). Estimates of mean density across focus areas ranged from 12.99—21.28 ha/singing male in 2008 to 7.04—9.43 ha/singing male in 2013. According to model estimates, there is a 0.992 probability that populations were growing (i.e., $\mu_{\theta 0}$ was positive) in our focal areas during this study and our model estimated hierarchical density-independent growth to be 35.7% annually ($\mu_{\theta 0}$=0.305, 0.114—0.498 95% BCI; $\sigma_{\theta 0}$=0.092, 0.004—0.310 95% BCI). The probability that populations were growing at each focal area was at least 0.996 and mean annual density-independent growth ranged from 28.1—40.5% across focus areas (Table 4, Figure 2). Regulation of growth rates by density was 3% and did not markedly affect population size over time (Figure 2; θ_1=-0.030, -0.051—-0.012 95% BCI).

Differences among focal areas were mostly defined by land composition. PCA resulted in 93.2% of variation among focal areas being explained by the first three axes. The variables dominating the first axis were land composition variables at the focus (perforfoc, peropnfoc) and landscape (perforlan, peropnlan) scales with the exception of drought. Axis two included more land composition metrics (perdevfoc, perdevlan), percrpfoc, winter, and SD compact. The third axis brought in important spatial metrics such as perinmgt, distmgt, and meanmgt.

DISCUSSION

Our focus areas successfully grew breeding populations of northern bobwhite over a 6-year period, and they lend strong support for the landscape-level habitat paradigm for restoration (Williams et al. 2004, Hernández et al. 2013). The Department's own history and experience reinforced the need to work beyond the local (farm) scale. Our areas exhibited a mean annual growth rate of 35.7% that directly contrasted with the 3% annual decline from Breeding Bird Survey data over a similar period (Sauer et al. 2014).

Few studies have demonstrated favorable responses to purposeful management at larger management scales (Brennan 2012). Our work represents one of the pioneering projects linking managed northern bobwhite habitat to population growth at the subcounty level. As such, it satisfied the primary goal established in KY's northern bobwhite restoration plan. Across the study period, the proportion of the areas managed for improved habitat ranged from 9 to 36%. If KDFWR was to establish a new focus area, then the probability of growing the

Table 4. Northern bobwhite (Colinus virginianus) mean population growth rate (log-scale, density independent) at each focus area in Kentucky, 2008-13

Focus Area	Growth rate	Lower 95% BCI	Upper 95% BCI	Probability of positive growth
Blue Grass Army Depot	0.325	0.142	0.513	0.998
Hart County CREP	0.340	0.166	0.519	0.998
Livingston County	0.328	0.132	0.535	0.998
Peabody WMA	0.247	0.057	0.427	0.986
Shaker Village	0.287	0.099	0.469	0.986

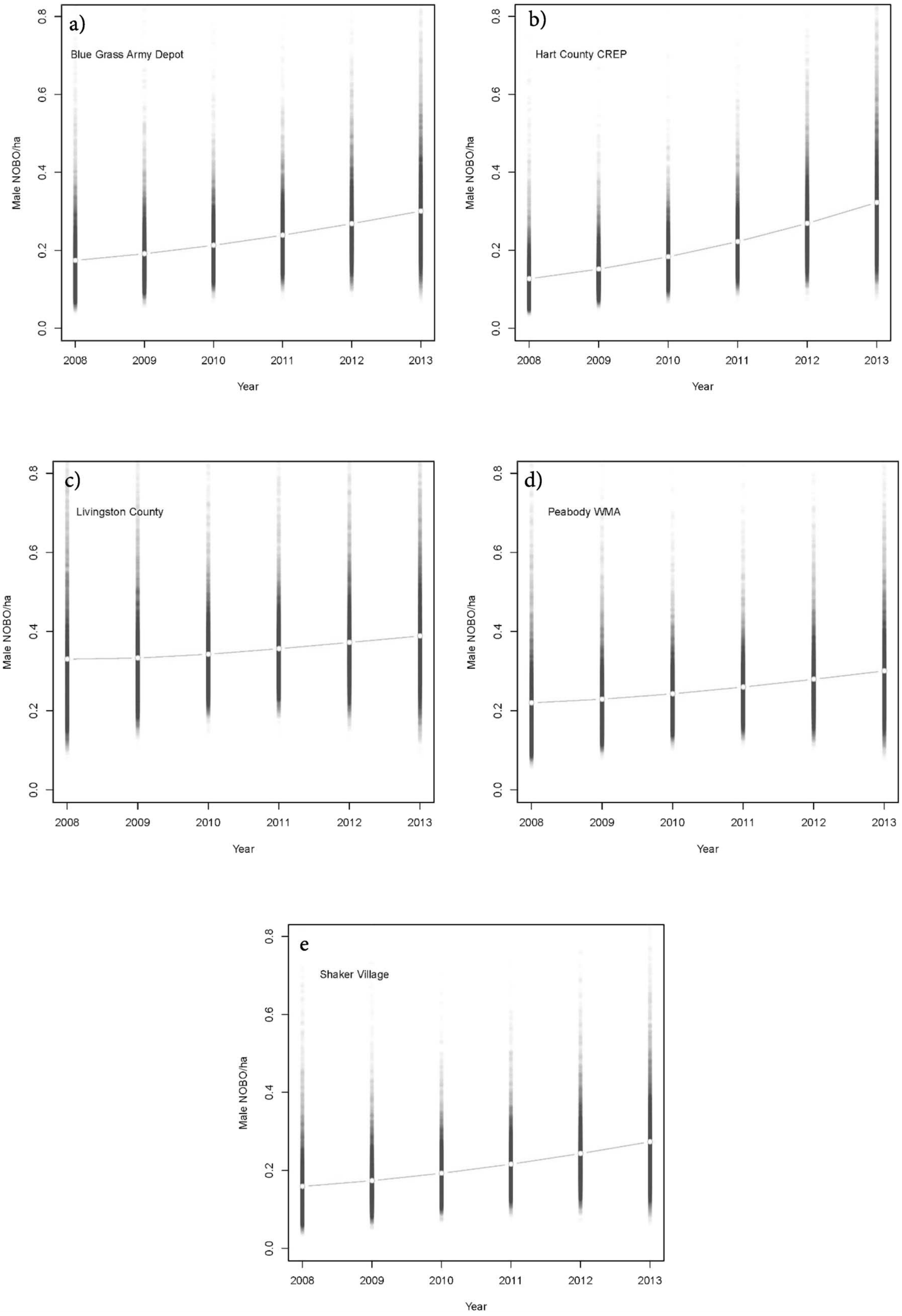

Fig. 2. The mean density and 95% BCI of breeding male northern bobwhite in five focus areas in Kentucky from 2008 to 2013.

population following similar guidelines is 99%. These results clearly demonstrated that we can successfully grow northern bobwhite breeding populations with a commitment to establishing and maintaining habitat. KDFWR has a powerful platform to share with the state's landowners that have an interest in northern bobwhite.

An understanding of what characterized our focus areas provides critical guidance for the future. Areas were in agricultural or non-forest dominated landscapes aligning with Riddle et al.'s (2008) recommendations. Peabody WMA was an exception (53% forested), but it was a reclaimed mineland site. The area's forest classification is not typical of prevailing forest cover (mature, closed-canopy hardwoods) and is characterized by open hardwood canopies with thick understories (Brooke et al. 2015). Despite the similarity in landscape composition at the coarse-scale, PCA results demonstrated that variability among our areas was largely explained by land cover composition within and outside the focus areas. Peabody forest composition may have confounded that analysis, but our results suggest that in non-forested landscapes, an array of land compositions can grow northern bobwhite breeding populations. Roseberry and Sudkamp (1998) modeled habitat suitability favoring 75 to 90% open lands. Open areas (row crops and grassland land cover) ranged from 35 to 85% in our focus areas, so we were successful growing northern bobwhite in more marginal environments. What appeared more important to northern bobwhite growth were the habitat management actions themselves. Management explained little of variation among the focus areas in our PCA. Hence, habitat management consistently produced northern bobwhite population growth across all our areas.

Twedt et al. (2007) noted targeting 5,000 ha areas with >200 northern bobwhite in the population for restoration. It is difficult to directly compare our first-year density estimates to this recommendation because 1) Twedt et al. (2007) assumed perfect detection of singing males and a constant relationship ($12x$) between a single singing male and its subsequent covey size, 2) Twedt et al. (2007) used a suite of land cover variables to predict abundance across space, and 3) if we were to extrapolate our density estimates beyond our point counts, we would be assuming no spatial heterogeneity in density. However, our results suggest that radical changes in landscape composition ($>10\%$) in short periods of time can jump start relatively low northern bobwhite densities in a variety of non-forested landscapes in Kentucky. Smaller areas can produce results if more dramatic habitat enhancements are completed. Shaker Village had substantial habitat enhancement (36%), but was only 1,160 ha.

Our analysis was limited by extreme variation among our focal areas and incomplete annual data. Areas were selected because of their unique attributes providing opportunities for northern bobwhite conservation. The diversity of prospects included mineland reclamation, Conservation Reserve Program land, Conservation Reserve Enhancement Program land, large-scale private lands prairie restorations, and a grazing operation. While diversity of management opportunities gives hope to the overall northern bobwhite restoration effort, it fosters a poor laboratory for study. Annual variability is a well-known attribute influencing northern bobwhite populations (Stoddard 1931, Roseberry and Klimstra 1984, Guthery 1997, Lusk et al. 2002). Our PCA analysis did highlight drought as an important variable explaining differences among our focus areas, so considering weather parameters should remain a core variable of future focal area assessment. With more powerful data, drought may have been able to explain variability within focal area northern bobwhite responses particularly when combined with habitat data (Webb and Guthery 1982, Rice et al. 1993). Our management actions were spatially accounted over the entire study period, but not for each individual year. That limited our ability to assess juxtaposition, relationship with weather, and an innumerable landscape metrics within the focus areas annually.

We agree with Williams et al. (2004) that harvest strategies should be implemented to avoid risking the primary goal of restoring northern bobwhite. We are confident that hunting was conservative across our study period. Public lands focus areas had controlled hunts that created low harvest rates ($< 20\%$), and frequent communication with landowners in Livingston County and Shaker Village also fostered low harvest rates. Hart County was the only area that we lacked any knowledge of hunting activity. If hunting is not controlled in focus areas, then it is imperative that data be collected to measure its effect on northern bobwhite population growth.

MANAGEMENT IMPLICATIONS

Purposeful management to grow northern bobwhite populations at the subcounty level has not been documented. A myriad of landowners, non-government organizations, universities, and government agencies have invested in efforts to restore northern bobwhite across the range. KY focus areas consistently grew northern bobwhite populations when radical changes ($\geq 10\%$ of the focus area) of new habitat were established and maintained. Small areas (approx. 1,000 ha) can be effective, but likely require more dramatic habitat enhancement. Selecting focus areas should take into account landscape composition (favoring agricultural, grassland, or non-closed canopy forested areas), offer significant opportunity for future management, and support existing populations of northern bobwhite (at least 44 ha/bird). Measures to control northern bobwhite harvest should be implemented, but if harvest is uncontrolled, standardized methods of collecting harvest information on public and private landscapes are an important need moving forward. Coordinated programs leveraging data across state lines foster powerful datasets to model the connection between landscape context, weather, management, harvest, and northern bobwhite density. It is imperative that management actions be spatially explicit (annually) to provide a full picture of how habitat management influences northern bobwhite population growth. Understanding the factors that drive northern bobwhite population growth in focus areas can inform future restoration efforts by minimizing risk and cost.

ACKNOWLEDGMENTS

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PROGRESS OF THE NATIONAL BOBWHITE CONSERVATION INITIATIVE

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ABSTRACT

Northern bobwhites (*Colinus virginianus*) have declined precipitously over 5 decades because of a decline in habitat, largely a result of agricultural intensification and inadequate management of natural plant succession. In response, quail biologists developed strategic and operational plans, and formed a national partnership of state and federal agencies, bobwhite institutions, non-government organizations, universities and private citizens. The early history of these efforts was reviewed in 2006 at the Sixth National Quail Symposium. Over the past 10 years, exponential growth occurred, including establishment of a home for national bobwhite conservation at the University of Tennessee, and funding from the National Fish and Wildlife Foundation, the United States Fish Wildlife Service Pitmann-Robertson (Federal Aid in Wildlife Restoration Program), individual state agencies and citizens. The result in 2016 is the National Bobwhite Conservation Initiative (NBCI), a 25-state consortium of state wildlife agencies and partners, led by the National Bobwhite Technical Committee and NBCI Management Board. In 2011, NBCI published an updated strategic restoration plan, and spatially-explicit planning tool, NBCI 2.0, followed in 2014 by an implementation plan, the NBCI Coordinated Implementation Program (CIP). We update the history of the NBCI, including changes in funding mechanisms, leadership, administration, and technical programs, and we assess current opportunities and the future of bobwhite conservation.

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Key words: northern bobwhites, *Colinus virginianus*, Pitmann-Robertson, conservation, plan

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THE INITIAL STAGES OF IMPLEMENTING THE WESTERN QUAIL MANAGEMENT PLAN

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ABSTRACT

The Western Association of Fish and Wildlife Agencies (WAFWA) established the Western Quail Working Group (WQWG) in July 2009. A memorandum of understanding (MOU) was signed by the western agencies responsible for quail management (Arizona, California, Colorado, Idaho, Kansas, Montana, Nevada, Oklahoma, New Mexico, Oregon, Texas, Utah, and Washington) as "a cooperative agreement to improve management and implement strategies for conservation of western quail and their habitats." The primary habitat management goals identified by the group are outlined in the Western Quail Management Plan, published by the Wildlife Management Institute in January 2010. Some of the past accomplishments of the WQWG, highlighted at recent WAFWA meetings, include shrub density reductions in New Mexico, riparian habitat restoration in Texas, private landowner habitat improvement cost-share in Kansas, and mesquite removal monitoring in Arizona. Management of western quail and their habitats has traditionally been accomplished on a relatively fine, local scale, so many of the current efforts to implement management practices identified in the plan are undocumented. A need identified by the WQWG is to better engage technical staff to guide outcomes and deliverables outlined in the plan. Additionally, the group is working to update the MOU to include Federal Land Management agencies, to better facilitate land management between state and federal agencies. A technical meeting with state and federal agency staff is scheduled for May 2017 in New Mexico to discuss state progress on implementing the Western Quail Management Plan, and how to increase state interest and efforts towards quail management. The discussions of the technical meeting will be presented at Quail 8.

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Key words: western quail, Western Quail Working Group, WQWG, Western Quail Management Plan, WAFWA

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POPULATION RESPONSE OF THREE QUAIL SPECIES TO HABITAT RESTORATION IN SOUTH TEXAS

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ABSTRACT

Maintaining and increasing usable space is paramount for maintaining and increasing wild quail. Aside from weather and other factors that can temporarily reduce densities, range-wide, no factor has as much influence on quail populations as the amount of habitat present across the landscape. In the field of quail management, "bad news" is the norm, as many articles begin by explaining how a select species has declined. Here we provide good news and use 4 empirical examples of population increases for 3 quail species following creation of usable space and restoration of patch connectivity. From 2008–2014, a suite of independent projects aimed at increasing usable space for quail was initiated across South Texas. These projects included 3 focused on northern bobwhites (*Colinus virginianus*), 1 focused on scaled quail (*Callipepla squamata*), and 1 landowner-executed project focused on Montezuma quail (*Cyrtonyx montezumae*). Through the correction of attributes limiting habitat, bobwhite numbers increased 22–378% across 2 studies. On one particular study site, native grassland restoration resulted in the colonization of bobwhites from adjacent areas to 1 bobwhite/1.2 ha from nearly 0. For scaled quail in South Texas, reducing buffelgrass standing crop via grazing from about 2,240 kg/ha to 1,008 kg/ha resulted in the recolonization of a previously unoccupied habitat patch to a density of 1 scaled quail/6 ha. Finally, clearing monotypic stands of the invasive native plant, ash juniper (*Juniperus ashei*) in the Edwards Plateau of Texas, resulted in the reestablishment of native grasses and forbs and thus recolonization by Montezuma quail from nearby areas. Although habitat restoration and management

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can be a painstaking and lengthy process, addressing limiting factors to quail occupancy is the only known way to increase wild quail populations. We hope that highlighting these particular studies will provide inspiration to those interested in restoring and increasing quail across the US.

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Key words: usable Space, habitat restoration, northern bobwhite, *Colinus virginianus*, scaled quail, *Callipepla squamata*, Montezuma quail, *Cyrtonyx montezumae*, South Texas

RESPONSE OF NORTHERN BOBWHITES TO HABITAT IMPROVEMENT ON PRIVATE LANDS IN THE ROLLING PLAINS OF TEXAS

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ABSTRACT

Northern bobwhites (*Colinus virginianus*) in the Rolling Plains of Texas have experienced significant declines in recent years. Examination of the Texas Parks and Wildlife Department Quail Roadside Counts reveals a steep decline since 2007 in the Rolling Plains of Texas. Biologists only detected 2.91 birds/counting route in 2013. This number marked 2 years in a row of record lows (counts started in 1978) below the long-term mean of 19.7 birds/route (Texas Parks and Wildlife 2015). These numbers are not surprising given the historically damaging drought Texas has suffered. Texas Parks and Wildlife Department counts improved to 7.5 bobwhites/counting route in 2014. This increase is linked to improving precipitation levels preceding and during the 2013 and 2014 breeding seasons. Though population growth is controlled primarily by rainfall (Jackson 1962), a reduction in the acreage of suitable habitat has also played a role in the bobwhite decline. Many areas on the Rolling Plains of Texas have become choked with invasive brush species, such as honey mesquite (*Prosopis glandulosa*) and juniper (*Juniperus* spp.), because of excessive grazing and a lack of fire (Mcpherson et al. 1988, Ansley et al. 1995). Asner et al. (2003) estimated woody cover increased as much as 500% in some areas of northern Texas between 1937 and 1999. Mesquite and juniper encroachment can occur to the point they become a steady-state, dominant vegetation that shades out grasses and other vegetation (Ansley and Weidemann 2008). Woody cover encroachment exceeding 70% canopy cover is not uncommon (Mirik and Ansley 2012). This heavy brush cover is not suitable habitat for bobwhites and limits population expansion even in years of adequate rainfall (Jackson 1969, Kopp et al. 1998). The millions of acres of brush-dominated rangeland in Texas represent areas that can become usable habitat for bobwhites when brush coverage is reduced to suitable levels. Mechanical removal using a dozer or track hoe is a common method of reducing canopy coverage of mesquite and juniper. This method allows a manager to selectively remove brush in the quantity and distribution that is desired while leaving beneficial shrub species such as lotebush (*Ziziphus obtusifolia*) or skunkbush sumac (*Rhus trilobata*) undamaged. We received funding from a Texas Parks and Wildlife Habitat Enhancement Grant to mechanically remove excessive brush cover on private lands with the objective of expanding bobwhite populations. We selected treatment sites that were currently inhabited by quail or were adjacent to sites inhabited by quail, but whose populations appeared to be limited by excessive brush cover and unable to expand or increase. These sites were located on ranches enrolled in The Quail-Tech Alliance research program. We treated 404 ha spread across 7 different properties during 2014 and 2015. Depending upon the site, brush removal was accomplished using either a bulldozer or track hoe to mechanically grub mesquite and juniper trees or in some instances a combination of both tree species. In some instances landowners used their own equipment while in others private contractors were hired to accomplish the reduction project. We worked with individual landowners to incorporate their overall wildlife management objectives. Consequently, the pattern and canopy coverage of brush remaining after mechanical reduction varied among projects and was influenced by the brush density of the treatment area. Some landowners removed strips of brush while others left brush mottes throughout the landscape. All projects resulted in increased acreage of suitable bobwhite habitat with a resulting brush canopy coverage ranging from 5% to 30% depending upon the project. The soil disturbance and subsequent beneficially timed rainfall caused treated areas to be revegetated with desirable forbs and grasses within 60 days posttreatment. Bobwhites were observed using the treatment areas within a few months of treatment. Though favorable rains in 2014 and 2015 played a role in this response, it would not have been possible for bobwhites to use the treatment areas before brush reduction. Bobwhite populations will positively respond to mechanical brush removal treatments in the Rolling Plains of Texas. This project increased the acreage of suitable habitat for bobwhites; showing the value of habitat restoration programs.

Citation: Dabbert, C. B., and R Verble-Pearson. 2017. Response of northern bobwhites to habitat improvement on private lands in the Rolling Plains of Texas. National Quail Symposium Proceedings 8:31–32.

Key words: brush reduction, *Colinus virginianus,* habitat management, northern bobwhite, Texas

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MONITORING NORTHERN BOBWHITE POPULATIONS REDUCES UNCERTAINTY ABOUT MANAGEMENT EFFECTIVENESS: A PARADIGM OF EMPIRICISM AND HOPE

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ABSTRACT:

Northern bobwhite (*Colinus virginianus*) populations have been declining across their range for decades because of habitat loss, degradation, and fragmentation. Habitat restoration and management—sometimes coupled with other cultural practices—has long been the paradigm for bobwhite conservation. However, the lack of peer-reviewed empirical evidence supporting the success of active management to increase bobwhite density and growth rates has created skepticism and uncertainty among some conservationists and user groups. Thus, our objectives were to test the basic prediction that active management can increase bobwhite populations across a large spatial extent and highlight the importance of population monitoring to refine management through adaptive feedback. We developed a Bayesian N-mixture model to estimate bobwhite densities and population growth rates at 17 Wildlife Management Areas (WMAs) in four Southeastern US states. Based on expert opinion, we classified WMAs into two groups—actively managed (e.g., bobwhite specific management) and passively managed (land management in a non-specific species fashion)—to test our prediction. Populations significantly increased across the survey periods at 4 WMAs and significantly decreased at 1 WMA. Populations on actively

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managed WMAs grew at an average of 13% per year, while populations on passively managed WMAs had stable trends. Mean bobwhite densities ranged from 0.145 (95% CrI: 0.025, 0.435) to 2.853 (95% CrI: 2.131, 3.914) birds/ha—typical of estimates in the literature. On WMAs where bobwhites are a management objective, continued population monitoring is vital to reduce uncertainty and make optimal management decisions to maintain recreationally viable populations. We provide a robust approach to estimate bobwhite densities and population trends in response to management so managers can make well-informed decisions and adapt in the future. We offer the conservation community some of the first empirical evidence of positive growth rates in bobwhite populations that should stimulate hope in bobwhite restoration.

Citation: Green, A.W., D. P. Grimes, G. Hagan, R. Hamrick, C. Harper, P. Keyser, J. Morgan, I. B. Parnell, R. Thackston, T. M. Terhune II and J. A. Martin. 2017. Monitoring northern bobwhite populations reduces uncertainty about management effectiveness: a paradigm of empiricism and hope. National Quail Symposium Proceedings 8:33–34.

Key words: adaptive management, Bayesian, *Colinus virginianus*, growth rates, monitoring, habitat management, uncertainty

FALL QUAIL DENSITIES ON PUBLIC LANDS IN MISSOURI: A DECADE OF MONITORING

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) fall population density has been determined annually since 2005 on 19 public land areas managed by the Missouri Department of Conservation (MDC). These demonstration areas, known as Quail Emphasis Areas (QEAs), were created as part of the MDC Strategic Guidance for Northern Bobwhite Recovery: 2003-2013. Management of QEA bobwhite populations, habitat and hunting has been evaluated periodically at the area, regional and statewide scale, and the program has been perpetuated in an updated 2014-2024 Strategic Guidance. QEAs were selected to represent MDC administrative regions and are highly variable in many aspects, e.g., size range from 298 to 3,642 hectares. QEAs are managed adaptively, maximizing usable space and early-successional plant communities, with bobwhite population density and distribution, and hunting, as response variables. Fall bobwhite calling coveys are measured with point transect surveys, distributed to cover nearly 100% of each QE, coveys are flushed to estimate covey size, and density is calculated with the Distance program. Observers, mostly permanent staff, initially received rigorous training, and periodic updates. Across QEAs and years, there has been a high amount of variability in weather and habitat management, and subsequently, population responses have been equally variable, as revealed by preliminary analysis for 2005-2010: (1) Number of covey observations on a QEA in a single year ranged from 0 to 178; (2) Encounter rate (i.e., number of coveys/effort) ranged from 0-5.95; (3) Density in areas where coveys were detected ranged from 0.003 coveys/ha to 0.103 coveys/ha (covey densities not adjusted for calling rate), and from 0.006 to 0.122 coveys/ha (covey densities adjusted for Missouri-specific calling rate); and (4) Some QEAs showed consistent declines in density from 2005-2010, whereas others increased. We discuss lessons learned from this long-term, state-wide effort to demonstrate effective quail management based on quantification of population response to prescribed management.

Citation: Emmerich, B.A. and T.V. Dailey. 2017. Fall quail densities on public lands in Missouri: a decade of monitoring. National Quail Symposium Proceedings 8:35.

Key words: *Colinus virginianus*, point transect surveys, public land, monitoring, Missouri, Program Distance, northern bobwhite

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EFFECTS OF BROAD-SCALE CONSERVATION ON NORTHERN BOBWHITE POPULATIONS IN AGRICULTURAL LANDSCAPES

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ABSTRACT

Private land initiatives such as the Conservation Reserve Enhancement Program (CREP) are avenues for broad-scale northern Bobwhite (*Colinus virginianus*) conservation. The CREP in Kentucky established 40,468 ha of native prairie grasses and riparian corridors in the Green River Basin. Northern bobwhite responses to similar conservation measures at local scales (i.e., the site of implementation) have been positive; however, the geographic extent of the influence of private land initiatives on populations is less understood. Our objectives were to investigate landscape-scale effects of CREP on northern bobwhite populations. Using a stratified random sampling design, 254 roadside point counts were performed over 5 years throughout the Green River Basin along a gradient of landscape-scale CREP density. Local-scale (500 m radius) CREP density was held constant at monitoring points. We analyzed data using an open-population distance sampling model that included estimators of appropriate landscape scale and strength of density dependence. Population response to the CREP was positive and outweighed conservation footprint. Our results suggest that broad-scale conservation can influence wildlife populations outside of targeted areas. Concurrently, because the majority of land in the Eastern U.S. is privately owned, private land conservation initiatives present an effective strategy for promoting wildlife population recovery across large areas. Our future directions with this research include improving model estimators, determining mechanisms behind landscape-scale effects of CREP, and determining the influence of the spatial arrangement of landscape features on local populations.

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Key words: northern bobwhite, Conservation Reserve Enhancement Program, broad-scale conservation, abundance estimation, private land initiatives

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MOLECULAR ECOLOGY OF NEW WORLD QUAILS: MESSAGES FOR MANAGERS

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ABSTRACT

Recent genetic studies of New World quails (Odontophoridae) have yielded important, and sometimes, counter-intuitive insights regarding their evolutionary relationships, genetic diversity, population structure, and biogeographic history. Many of these new insights have important implications for managers. New World quails are a distinct family within galliforms, most closely related to guineafowl (Numididae) and pheasants (Phasianidae) rather than guans and chachalacas (Cracidae). The African stone partridges (*Ptilopachus* spp.) are the closest living relatives of the New World quails. The combination of phylogeographic studies with ecological niche modeling has revealed the biogeographic history of several species of New World quails, including Pleistocene refugia and post-Pleistocene range expansions, contractions, or stasis. Divergence times within and among genera often date to climactic or geologic events 1–5 million years ago. The many subspecies of quail described over the past 100 years were based on minor differences in plumage and probably represent artificial sectioning of latitudinal clines rather than historically isolated and evolutionary distinct units. Subspecies are often used as proxies for management units, but conservation efforts directed at the northern bobwhite (*Colinus virginianus*) and scaled (*Callipepla squamata*), California (*C. californica*), and Gambel's (*C. gambelii*) quails may not benefit from such an approach. Ecological regions, rather than subspecies, are probably more appropriate as a "management unit." The overall lack of population structure, evidence of long-distance dispersal and historical gene flow among populations, and the cyclical population dynamics of these species suggest that there is a biological basis for conserving large blocks of interconnected habitat. Focal areas of restoration projects should be spatially extensive and interconnected to facilitate dispersal and recolonization. With a better understanding of how quail populations responded to past climactic conditions, we are better able to predict how quail may respond to future conditions and ensure the conservation of these iconic New World birds.

Citation: Williford, D., R. W. DeYoung, and L. A. Brennan. 2017. Molecular ecology of New World quails: messages for managers. National Quail Symposium Proceedings 8:37–56.

Key words: landscape genetics, New World quails, Odontophoridae, phylogenetics, phylogeography, population genetics, taxonomy

The New World quails (Odontophoridae) are a family of gallinaceous birds, consisting of 2 subfamilies, 10 genera, and 33 species (Table 1). The family has a broad distribution in the Western Hemisphere, from the United States to northern Argentina (Fig. 1). Many quails are popular game birds or are subject to subsistence hunting (Madge and McGowan 2002). The northern bobwhite (*Colinus virginianus*) has been the subject of numerous ecological and behavioral studies because of its wide geographic distribution and popularity as a game bird; it is fair to say that it is the best-known New World quail (Rosene 1969, Lehmann 1984, Hernández et al. 2002, Brennan 2007, Brennan et al. 2014). California (*Callipepla californica;* Leopold 1977, Calkins et al. 2014), Gambel's (*C. gambelii;* Gee et al. 2013), scaled (*C. squamata;* Dabbert et al. 2009), mountain (*Oreortyx pictus;* Gutíerrez and Delehanty 1999), and Montezuma quails (*Cyrtonyx montezumae,* Stromberg 2000) are also relatively well-studied within the United States. Less is known about the ecology of the northern bobwhite and California, Gambel's, scaled, and Montezuma quails in México, or the species of quails restricted to Central and South America (Johnsgard 1988, Carroll and Eitniear 2000, Madge and McGowan 2002, Hernández et al. 2014).

Most studies of quail that include a phylogenetic or biogeographic component begin with a summary of currently accepted taxonomy, followed by a confusing and contradictory history of nomenclature and end with statements about the lack of consensus among taxonomists (Gutíerrez et al. 1983, Gutíerrez 1993, Johnsgard 1988, Zink and Blackwell 1998, Eo et al. 2009). To many wildlife biologists, taxonomic arguments must seem like little more than bureaucratic infighting among a small

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constituency that operates out of dusty museum drawers, heard but not seen. In reality, taxonomy is the key for understanding how past events have shaped current populations and their distribution. Furthermore, subspecies are often used as proxies for conservation and management units, but conservation policies based outdated taxonomies may waste resources and result in the loss of evolutionarily distinct lineages (Laerm et al. 1982, Avise and Nelson 1989, Zink 2004, Haig and D'Elia 2010, Prie et al. 2012). The root of taxonomic confusion among New World quails and other avian taxa is that many subspecies were historically based on small sample sizes, specimens collected outside the breeding season, minor phenotypic variation, and difficulty in determining whether subspecific taxa represented discrete units or clinal variation over broad geographic areas (Remsen 2005, Rising 2007, Winker 2010). The resolution of taxonomic confusion within the New World quails, especially at the levels of species and subspecies, has been a conservation priority for more than 2 decades (Gutíerrez 1993; Carroll and Eitniear 2000, 2004; Madge and McGowan 2002). This has begun to change in the past decade, as wildlife biologists have turned to molecular tools to answer questions about population structure, dispersal, mating strategies, and the effects of harvest and restocking (DeYoung and Honeycutt 2005, Latch et al. 2005, Scribner et al. 2005, Oyler-McCance and Leberg 2012). Molecular genetics has recently been applied to studying the relationship between landscape and dispersal in northern bobwhites (Terhune 2008; Eo et al. 2010; Berkman et al. 2013a, b; Miller 2014; Williford et al. 2014a) and the potential effects of bobwhite restocking efforts on wild populations (Ellsworth et al. 1988, Nedbal et al. 1997, Evans et al. 2009). Recent phylogenetic studies have begun to resolve long-standing questions regarding the evolutionary relationships of New World quails and species limits within Odontophoridae genera, and, most importantly, the ecological and biogeographical drivers of species and adaptation (Zink and Blackwell 1998; Cohen et al. 2012; Williford et al. 2014a, b, c, 2016; Hosner et al. 2015). An understanding of how past events have shaped the present can help wildlife biologists prioritize conservation efforts and enables prediction of future changes in climate and habitat and their effects on populations of quail and other game species (Avise 2004, DeYoung and Honeycutt 2005, Oyler-McCance and Leberg 2012).

Our objective was to review and synthesize genetic analyses of quail taxa and populations, and translate these reports into information relevant to the management of New World quails. We focus on phylogenetic relationships, species limits, phylogeography, and population genetics; and highlight the history and trends in genetic research on New World quails and their importance to managers. We also include a table of pertinent terms and their definitions (Table 2) as well as geological timescales detailing important events in the evolution of New World quails (Figs. 2 and 3). We conclude with a reflection of what has been learned and provide future directions for research.

Table 1. Taxonomy of the New World quails (Odontophoridae) based on AOU (1998), Madge and McGowan (2002), Bowie et al. (2013), Clements et al. (2015), Hosner et al. (2015), Remsen et al. (2015). The number of subspecies listed for each species are from Madge and McGowan (2002) except for the northern bobwhite and scaled, California, Gambel's, mountain, and Montezuma quails, which follow Brennan et al. (2014), Dabbert et al. (2009), Calkins et al. (2014), Gee et al. (2013), Gutíerrez and Delehanty (1999), and Stromberg (2000), respectively.

- African stone partridges – Subfamily Ptilopachinae[a]
  - Stone partridges (*Ptilopachus,* 2 species)
    - Stone partridge (*P. petrosus*)
    - Nahan's francolin (*Pternistis nahani*)
- New World quails – Subfamily Odontophorinae
  - Tawny-faced quails (*Rhynchortyx,* 1 species)[b]
    - Tawny-faced quail (*R. cinctus,* 3 subspecies)
  - Harlequin quails (*Cyrtonyx,* 2 species)
    - Montezuma quail (*C. montezumae,* 4 subspecies)
    - Ocellated quail (*C. ocellata*)
  - Singing quails (*Dactylortyx,* 1 species)
    - Singing quail (*D. thoracicus,* 17 subspecies)
  - Wood quails (*Odontophorus,* 15 species)
    - Marbled wood-quail (*O. gujanensis,* 8 subspecies)
    - Spot-winged wood-quail (*O. capueira,* 2 subspecies)
    - Black-faced wood-quail (*O. melanotis,* 2 subspecies)
    - Rufous-fronted wood-quail (*O. erythrops,* 2 subspecies)
    - Black-fronted wood-quail (*O. atrifrons*)
    - Chestnut wood-quail (*O. hyperythrus*)
    - Dark-backed wood-quail (*O. melanonotus*)
    - Rufous-breasted wood-quail (*O. speciosus,* 3 subspecies)
    - Tacarcuna wood-quail (*O. dialeucos*)
    - Gorgeted wood-quail (*O. strophium*)
    - Venezuelan wood-quail (*O. columbianus*)
    - Black-breasted wood-quail (*O. leucolaemus*)
    - Stripe-faced wood-quail (*O. balliviani*)
    - Starred wood-quail (*O. stellatus*)
    - Spotted wood-quail (*O. guttatus*)
  - Mountain quails (*Oreortyx,* 1 species)
    - Mountain quail (*O. pictus,* 5 subspecies)
  - Tree-quails (*Dendrortyx,* 3 species)
    - Bearded tree-quail (*D. barbatus*)
    - Long-tailed tree-quail (*D. macroura,* 6 subspecies)
    - Buffy-crowned tree-quail (*D. leucophrys,* 2 subspecies)
  - Banded quails (*Philortyx,* 1species)
    - Banded quail (*P. fasciatus*)
  - Crested quails (*Callipepla,* 4 species)
    - Scaled quail (*C. squamata,* 4 subspecies)
    - Elegant quail (*C. douglasii,* 5 subspecies)
    - Gambel's quail (*C. gambelii,* 4 subspecies)
    - California quail (*C. californica,* 5 subspecies)
  - Bobwhites (*Colinus,* 3 species)
    - Northern bobwhite (*C. virginianus,* 18 subspecies)
    - Black-throated bobwhite (*C. nigrogularis,* 4 subspecies)
    - Crested bobwhite (*C. cristatus,* 20 subspecies)[c]

[a] See Bowie et al. (2013) for information. Multilocus phylogenetic analysis indicates that *Ptilopachus* is more closely related to Odontophoridae than to any other galliforms (Crowe et al. 2006, Cohen et al. 2012, Hosner et al. 2015).

[b] Results of multilocus phylogenetic analysis indicate that the tawny-faced quail is a sister clade to all of the other species of Odontophorinae (Hosner et al. 2015).

[c] Madge and McGowan (2002) and Johnsgard (1988) considered the 6 subspecies in northern Central America to represent a distinct species, the spot-bellied bobwhite (*Colinus leucopogon*). However, genetic data do not support this taxonomic view (Williford et al. 2016); thus, we use the species taxonomy presented in AOU (1998), Clements et al. (2015), and Remsen et al. (2015).

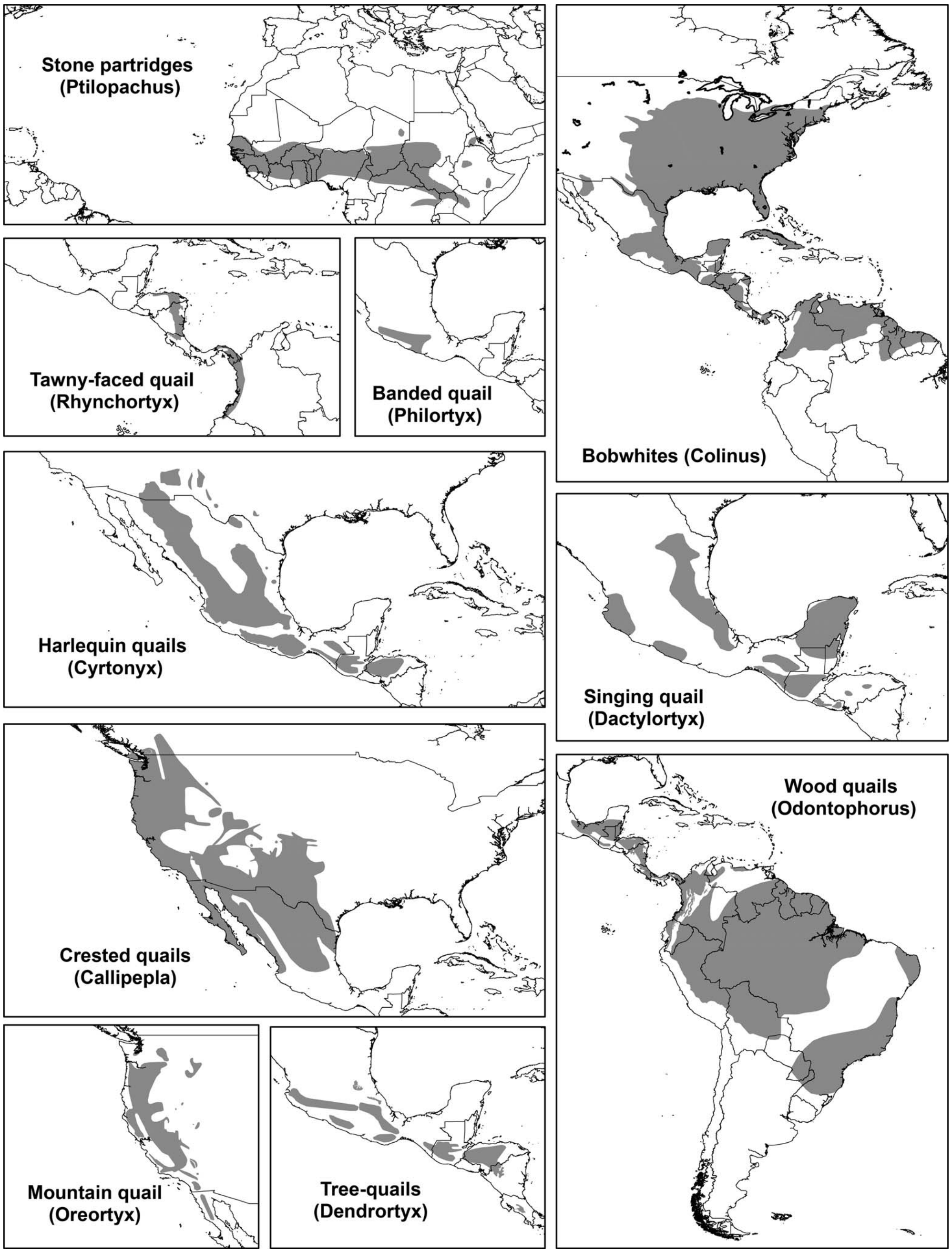

Fig. 1. Geographic ranges of the New World quail (Odontophoridae) genera. Recent phylogenetic studies have shown that the African stone partridges (*Ptilopachus*) are more closely related to New World quails than to other galliforms (Crowe et al. 2006, Cohen et al. 2012, Hosner et al. 2015). Range maps were constructed from shapefiles available from BirdLife International and NatureServe (2015).

HIGHER PHYLOGENETICS AND SYSTEMATICS

The terms phylogenetics and systematics are often used interchangeably, yet represent distinct disciplines. Phylogenetics is the study of evolutionary relationships among organisms (Brinkman and Leipe 2001), whereas systematics is more concerned with their taxonomic classification (Mayr 1999). Throughout much of the history of modern biology, scientists were restricted to morphology and other phenotypic traits in the study of evolutionary relationships and the biological classification of organisms. Phylogenetics and systematics based on phenotypic traits were sometimes confounded by the retention of ancestral traits, or the independent evolution of similar traits among either distantly related or closely related taxa; these events are termed plesiomorphy, convergence, and parallelism, respectively (Collard and Wood 2000, van Tuinen et al. 2001, Wiens et al. 2003, Gaubert et al. 2005, Pereira and Baker 2005). For example, convergent evolution has played havoc with systematics of birds of prey. Taxonomists placed falcons, caracaras, kites, hawks, eagles, and Old World vultures in a single order, Falconiformes, because of the overall

Table 2. Common terms and definitions used in phylogenetics, phylogeography, and population genetics and genomics (after Futuyma 1998; Avise 2000, 2004; Hey and Machado 2003; Noor and Feder 2006; Ranz and Machado 2006; Ricklefs 2007; Lemey et al. 2009; Bansal et al. 2010; Peterson et al. 2011; Yandell and Ence 2012; dos Reis et al. 2016).

Term	Definition
adaptive variation	Genetic variation that is associated with morphological, physiological, biochemical, or behavioral traits that influence survival and reproductive success.
allopatric	Of a population or species, occupying a geographic region different from that of another population or species.
allozyme	Co-dominant nuclear DNA that consists of enzymes that differ in their mobility on a charged gel.
annotated	Refers to the process of identifying genes within a sequenced genome.
basal	In phylogenetics, refers to a branch of a phylogenetic tree that is closer to the root of the tree in comparison with another branch.
clade	An evolutionary assemblage that includes a common ancestor and all of its descendants.
cladogram	A branching diagram depicting the relationships among organisms and the relative sequence in which they evolved from common ancestors.
clinal variation	Gradual variation in a trait over a geographical area that is associated with an environmental gradient.
convergent evolution	The evolution of similar features independently in different evolutionary lineages, usually from different antecedent features or by different evolutionary pathways.
DNA–DNA hybridization	A method used to estimate genetic distance between 2 species based on the similarity of pools of single-stranded DNA from each species.
DNA polymorphism	Any difference in the nucleotide sequence of a gene among individuals.
ecological niche model	Estimation of the area that is abiotically suitable for a species based on occurrence records and the relationship of those records to environmental variables.
evolutionary conservatism	The retention of ancestral features among closely related lineages over long periods of time.
fossil calibration	Constraints on timing of lineage divergence in molecular clock dating. These are established through fossil-based minimum and maximum constraints on the ages of specific clades.
genome	All of the genetic information an organism carries. In animals, genetic information is derived among the nuclear and mitochondrial genomes.
genomic library	A collection of total genomic DNA from a single organism.
landscape genetics	The science of understanding how contemporary geographical and environmental features structure genetic variation at both the population and individual levels.
lineage	A series of ancestral and descendant populations or species, through time.
haplotype	A unique DNA sequence from a haploid genome such as the mitochondrial genome.
haplotype diversity	A measure of genetic diversity that quantifies the relationship between no. of haplotypes and their individual frequencies in a population.
Last Glacial Maximum (LGM)	The last period of the last major glaciation, the Wisconsin Glaciation, 85,000–11,000 yr ago, when the ice sheets were at their greatest extension. The LGM lasted from 26,500 to 19,000 yr ago, with the glaciers reaching their maximum position around 24,500 yr ago.
microsatellite DNA	Co-dominant nuclear DNA markers that consist of sets of short, repeated nucleotide sequences. Also known as short tandem repeats.
mitochondrial DNA (mtDNA)	DNA that is part of the mitochondrial genome.
mitochondrial genome	All of the genetic information located in the mitochondrion, the intracellular organelle that releases energy from food molecules. In most animals, the mitochondrial genome is a small ring of DNA that varies from 16,000 to 17,000 base pairs.
model organism	A species that has been widely studied because it is easy to maintain and breed in a laboratory setting and has particular experimental advantages. Examples of model organisms include the baker's yeast (*Saccharomyces cerevisiae*), the common fruit fly (*Drosophila melanogaster*), zebrafish (*Danio rerio*), chicken (*Gallus gallus*), and the brown rat (*Rattus norvegicus*).
monophyletic	A group that includes all the descendants of a single common ancestor.
multilocus	In animals, genetic data derived from nuclear and mitochondrial genome
neutral marker	A genetic marker that is not influenced by natural selection, but is instead influenced by demographic processes and chance.
nucleotide diversity	A measure of genetic diversity that quantifies the average nucleotide differences between individuals in a population.
nuclear DNA	DNA that is located in the nucleus of a cell.
	All of the nuclear genetic information an organism carries. The nuclear genome contains most of an organism's genes. Nuclear genomes vary greatly in size from 130 billion base pairs in the marbled lungfish (*Protopterus aethiopicus*) to 385 million base pairs in the green-spotted pufferfish (*Tetraodon nigroviridis*). Humans have a nuclear genome of 3.2 billion base pairs.
parallel evolution	The evolution of similar or identical features independently in related lineages, thought usually to be based on similar modification of the same developmental pathways.

Table 2. Continued.

Term	Definition
phenotypic	Pertaining to the morphological, physiological, biochemical, or behavioral traits of an organism.
phylogenetic tree	A branching diagram depicting the relationships among organisms and the relative sequence in which they evolved from common ancestors.
phylogenetics	The study of evolutionary relationships among organisms.
phylogeny	The evolutionary relationships among lineages in a clade, illustrated by the pattern of branching in a phylogenetic tree.
phylogeography	The study of the principles and processes that have influenced the historical geographic distributions of genetic lineages within a species or closely related species.
population expansion	Increase in the no. of individuals in a population, usually accompanied by an increase in genetic variation.
population structure	Composition of a population or group of populations. In phylogeography and landscape genetics, population structure refers the relationship between geographic distance and genetically distinct groups. Population structure is said to be strong when geographically distant populations also exhibit high degree of genetic differentiation, whereas population structure is weak genetic differentiation is low or lacking regardless of the geographic distance.
restriction-fragment length polymorphism (RFLP)	A variant of a DNA sequence that is generated through the gain or loss of a restriction site due to a DNA substitution. RFLP analysis involves cutting DNA with $\geq$1 endonucleases, separation of the fragments by molecular weight via gel electrophoresis, and visualizing the size-sorted fragments.
single nucleotide polymorphisms (SNPs)	Short segments of DNA in which variation is the result of a single nucleotide substitution.
sister clade	A pair of clades descending from a single common ancestor.
supertree analysis	A phylogenetic method that combines small phylogenetic trees with incomplete species overlap to build comprehensive species phylogenies.
systematics	A branch of biology that deals with the classification of living organisms on the basis of their evolutionary relationships.
taxon (plural = taxa)	A monophyletic group of organisms that can be recognized by sharing a definite set of derived characteristics.
taxonomic unit	A specific taxon.
taxonomy	Description and classification of organisms.
transcriptome	The complete set of transcribed RNA elements of the genome.

morphological similarity. However, phylogenetic studies based on molecular data revealed that falcons were more closely related to songbirds (Passeriformes) and parrots (Psittaciformes; Ericson et al. 2006, Hackett et al. 2008). This revelation led taxonomists to restrict the use of Falconiformes to falcons and caracaras, and erect a new order for the remaining birds of prey (Chesser et al. 2010, 2016). These findings suggest that the strong morphological similarity between falcons and hawks was due to independent adaptations to similar niches. The development of molecular genetic markers in the 1960s revolutionized the study of evolution and taxonomy. Advances in computing technology and laboratory techniques in the past 3 decades have resulted in a proliferation of new molecular markers and analytical methods, including the analysis of complete genomes (DeYoung and Honeycutt 2005, Hauser and Seeb 2008, Oyler-McCance and Leberg 2012, McCormack et al. 2013). Morphological phylogenetics will continue to be needed to understand the evolutionary relationships of prehistoric taxa, of which only fossils remain (Jenner 2004, Wiens 2004); however, the study of phylogenetic and systematic relationships among extant organisms, especially at the genus, species, and population levels, now relies heavily on molecular data (Avise 2004, Edwards 2009).

Extant members of Galliformes are divided into 5 families: Megapodiidae (mound-builders and brush turkeys), Cracidae (currasows, chachalacas, and guans), Numididae (guineafowls), Phasianidae (pheasants, peafowl, grouse, turkeys, and junglefowl), and Odontophoridae (Crowe et al. 2006, Kriegs et al. 2007, Wang et al. 2013, Kimball and Braun 2014). Numididae, Phasianidae, and Odontophoridae, collectively referred to as phasionoids, are one another's closest relatives (Crowe et al. 2006, Kriegs et al. 2007). The most closely related avian order to galliforms is Anseriformes (ducks, geese, swans, and screamers), and these 2 orders form the clade Galloanserae (Sibley et al. 1988, Groth and Barrowclough 1999, Mindell et al. 1999, Zusi and Livezey 2000, Chubb 2004). Galloanserae is the sister clade to Neoaves, which includes all other extant birds except ratites and tinamous. Galloanserae and Neoaves together form Neognathae, a sister clade to Palaeognathae (ratites and tinamous). Neognathae and Paleognathae are collectively referred to as the Neornithes, itself part of a larger clade, Ornithurae, which also includes numerous prehistoric birds (Naish 2012).

Early attempts using molecular data to estimate the timing of the divergence of modern avian taxa often resulted in Late Cretaceous–age (100–65 million yr ago [MYA]) dates for many avian orders and families, including Galliformes (Cooper and Penny 1997, van

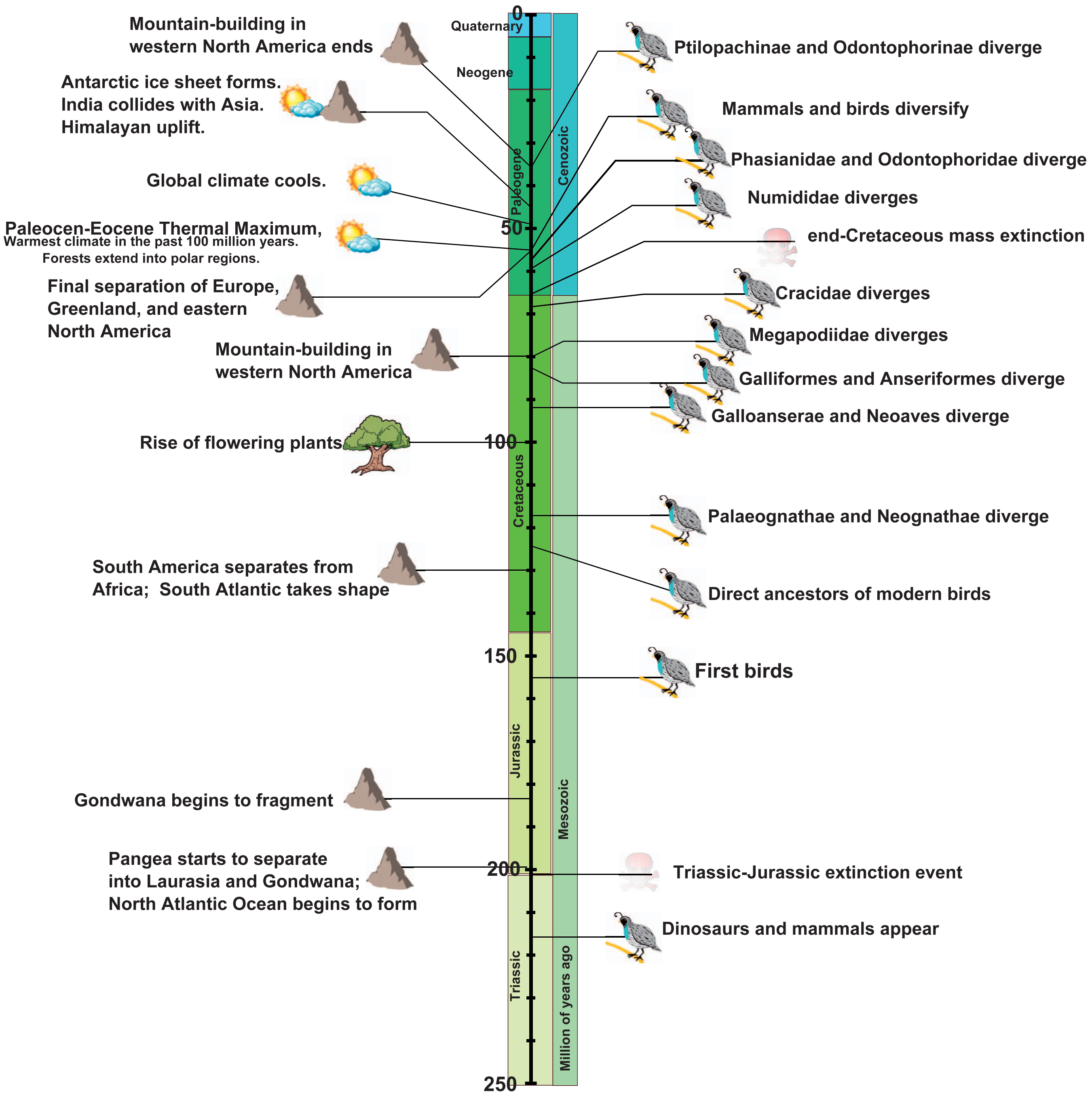

Fig. 2. Timeline of important events related to the evolution of New World quails during the Mesozoic and early Cenozoic eras. The Mesozoic Era is divided into 3 periods: Triassic (252–201 million yr ago [MYA]), Jurassic (201–145 MYA), and Cretaceous (145–66 MYA). The Cenozoic is divided into 3 periods: Paleogene (66–23 MYA), Neogene (23–2.58 MYA), and Quaternary (2.58 MYA to present).

Tuinen and Hedges 2001, van Tuinen and Dyke 2004, Crowe et al. 2006, Brown et al. 2008). For example, the divergence estimate of Cracidae from Phasianidae was estimated to 80 MYA (van Tuinen and Hedges 2001, van Tuinen and Dkye 2004). Crowe et al. (2006) arrived at an estimate of 49.6–52.0 MYA for the origin of Odontophoridae. In contrast, the oldest fossils that can be reliably identified as belonging to modern orders and families are restricted to deposits to mid-Cenozoic deposits (∼35 MYA), which suggests that most modern avian taxa originated and diversified after the end-Cretaceous extinction event (66 MYA; Mayr 2005, 2009, 2014; Longrich et al. 2011; Ksepka and Boyd 2012). Avian fossils from Cretaceous, Paleocene, or Eocene deposits that have been ascribed to modern orders and families are often fragmentary and poorly preserved (Mayr 2005, 2009). One exception to this is the Cretaceous fossil *Vegavis iaai,* which has been shown to fit within Anseriformes (Clarke et al. 2005, Ksepka and Clarke 2015). The discrepancy between molecular divergence

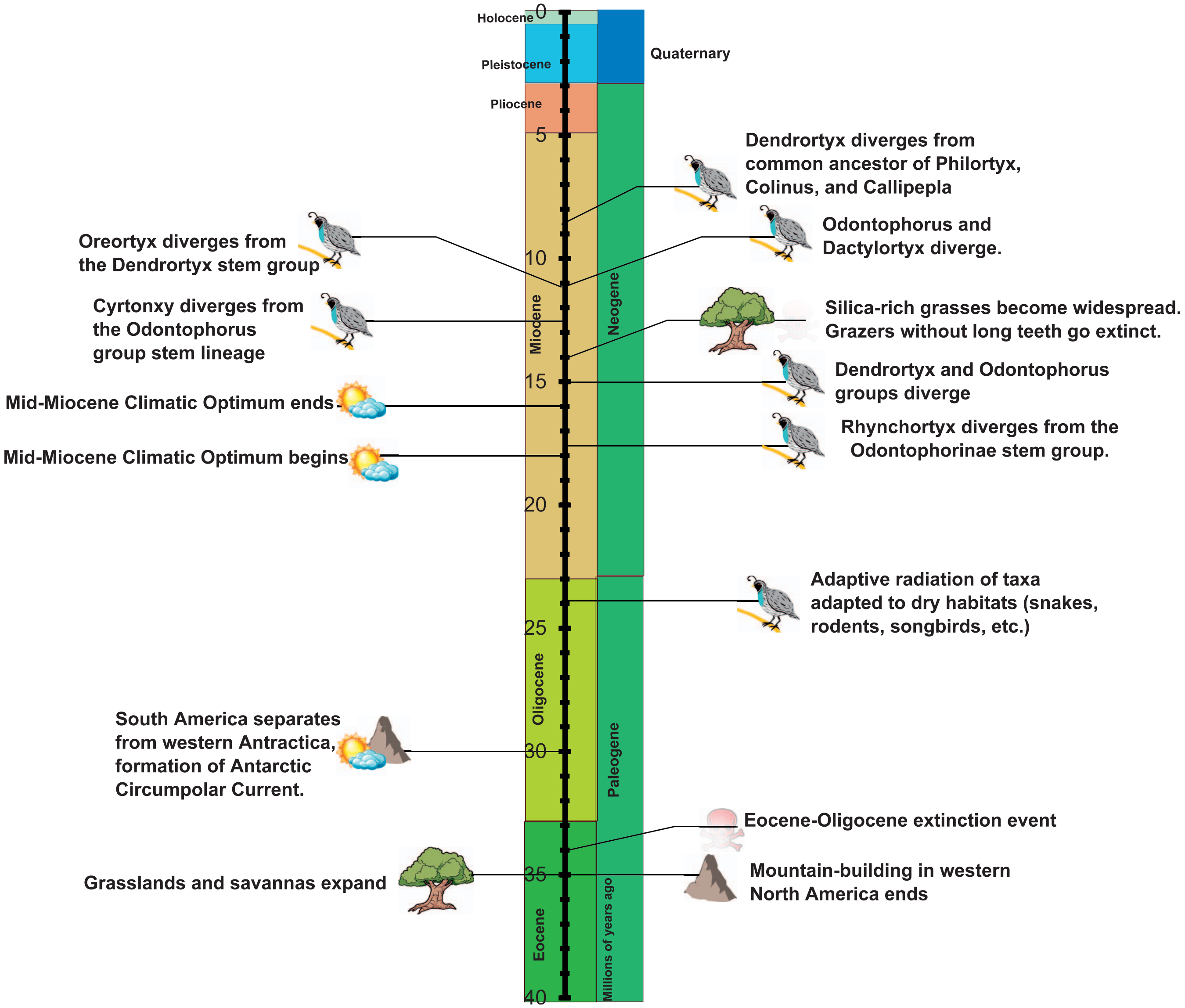

Fig. 3. Timeline of important events related to the evolution of New World quails during the middle and late portions of the Cenozoic Era (40–8 million yr ago).

estimates and the fossil record may be due partially to the incompleteness of the fossil record, the fragility of avian skeletons, and that early representatives of modern orders may not have lived in habitats where fossilization was likely to occur (Smith and Peterson 2002, Brocklehurst et al. 2012). Other sources for the discrepancy include rapidity of diversification among Neornithes, variable mutation rates among different molecular markers, and parameters specified in the used in divergence estimation (Ho and Phillips 2009, Ksepka et al. 2014, Ksepka and Phillips 2015). Lastly, the misidentification and misclassification of avian fossils and the use of the wrong fossils to calibrate nodes within a phylogenetic tree may also have contributed to more ancient divergence dates inferred from molecular data (Mayr 2009, Ksepka 2009, Ksepka et al. 2014). For example, fossil taxa *Gallinuloides wyomingensis* and *Amitabha urbsinterdictensis* have been used in multiple studies to calibrate divergences of modern galliform families (van Tuinen and Dyke 2004, Crowe et al. 2006, Pereira and Baker 2006, Cox et al. 2007). However, re-examination of fossil material of both species revealed that *G. wyomingensis* was a basal member of Galliformes and thus not a suitable fossil calibrate the divergence of any modern family, and *A. urbsinterdictensis* was more closely related to rails (Rallidae) and not a galliform (Ksepka 2009). Recently, a consensus has been reached on some aspects of the evolution and timing of the divergence of Galliformes and modern families. The unequivocal placement of *V. iaai* within Anseriformes is evidence for a Late Cretaceous origin of both anseriforms and galliforms, as well as, the initial Palaeognathae–Neognathae split, which has been confirmed by several recent studies using multilocus data sets and more conservative fossil calibrations (Jarvis et al. 2014, Ksepka and Phillips 2015, Stein et al. 2015, Wang et al. 2016 but see Ericson et al. 2006 and Prum et al.

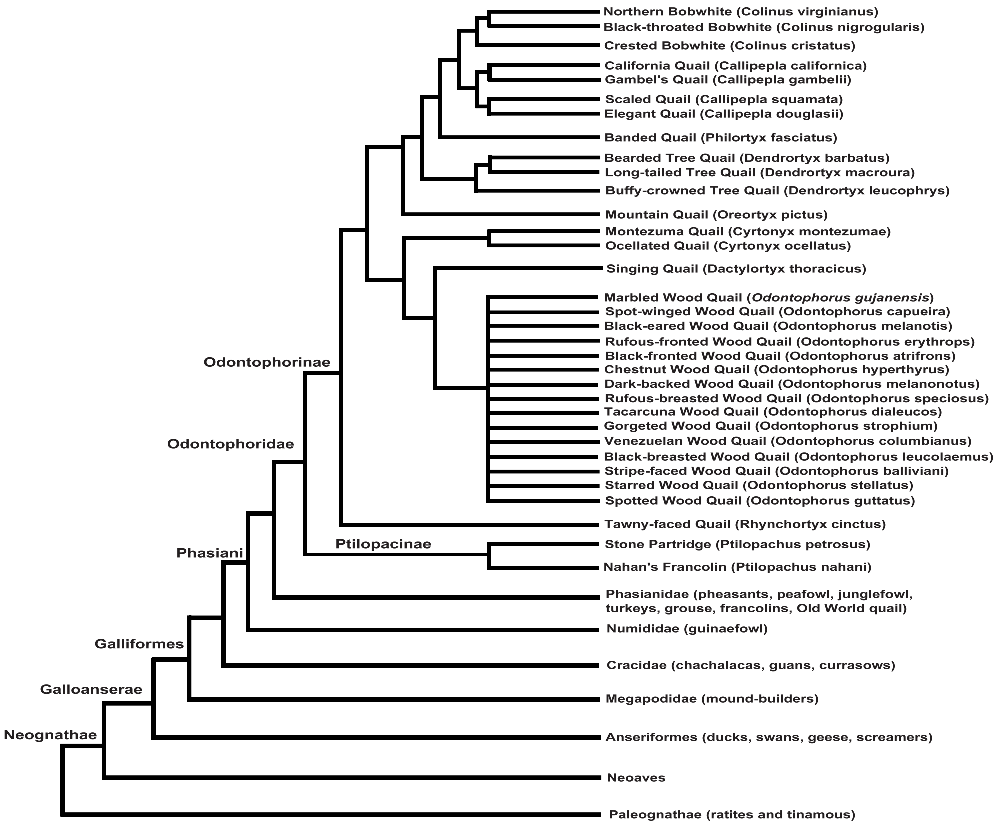

Fig. 4. A cladogram depicting the evolutionary relationships of New World quails based on the results of recent molecular studies (Crowe et al. 2006, Cohen et al. 2012, Williford 2013, Hosner et al. 2015, Williford et al. 2016). No phylogenetic study of New World quails has included all 15 species of wood quails (*Odontophorus* spp.); however, genetic data (Hosner et al. 2015) do not support Johnsgard's (1988) hypothesized species relationships based on plumage coloration. On account of uncertainty regarding the phylogenetic relationships among the wood quails, we chose to depict the *Odontophorus* as a polytomy (an internal node of cladogram that has >2 immediate descendants).

2015 for alternative scenarios). Several studies have upheld a Late Cretaceous origin for Megapodiidae and either a Cretaceous or early Cenozoic origin for Cracidae (Stein et al. 2015, Hosner et al. 2016, Wang et al. 2016). The timing of the origin of the phasionoids (Numididae, Phasianidae, and Odontophoridae) remain unclear but recent studies point to either a Cretaceous or early Cenozoic split from Cracidae followed by divergence of Numididae, Phasianidae, and Odontophoridae during the Paleocene and Eocene (Stein et al. 2015, Wang et al. 2016).

The distinctiveness and monophyly of the New World quails among galliforms has been supported by both morphological (Holman 1961, 1964; Dyke et al. 2003) and molecular data (Gutíerrez et al. 1983, Sibley and Ahlquist 1990, Randi et al. 1991, Cox et al. 2007, Kriegs et al. 2007). Morphological characters unique to New World quails include 1) short, stout bills with a curved culmen and serrated mandibular tomium; 2) bare nostrils; 3) hallux above the other toes; 4) lack of tarsal spurs; and 5) 4–10 rectrices (Holman 1961, Johnsgard 1988, Sibley and Ahlquist 1990). Traditional taxonomy based on morphological data, however, often classified New World quails as a subfamily within Phasianidae (historical review by Sibley and Ahlquist 1990, see also Dyke et al. 2003). The results of osteological analysis (Holman 1961, 1964) and DNA–DNA hybridization studies (Sibley et al. 1988, Sibley and Ahlquist 1990) gradually led to the recognition and acceptance of New World quails as a distinct family within Galliformes (American Ornithologists' Union [AOU] 1998). Early molecular phylogenetic analyses suggested that Odontophoridae had a basal relationship to guineafowl (Numididae; Sibley and Ahlquist 1990, Randi et al. 1991, Kornegay et al. 1993, Kimball et al. 1999, Armstrong et al. 2001). More recent studies based on large, multilocus data sets indicate that New World quails are more closely related and basal to Phasianidae, and that these 2 families are a sister clade to Numididae (Crowe et al. 2006, Cox et al. 2007, Kriegs et al. 2007, Wang et al. 2013; Fig. 4).

Modern phylogenetic analyses also provide greater nuance to the biogeography of New World quails. The most surprising finding in recent years has been that the closest living relatives of New World quails are 2 African galliforms, the stone partridge (*Ptilopachus petrosus*) and Nahan's francolin (*Pternistis nahani*); this relationship is strongly supported by the analyses of mitochondrial and nuclear DNA (Crowe et al. 2006, Cohen et al. 2012, Hosner et al. 2016, Wang et al. 2016). Odontophoridae is now organized as 2 subfamilies: *Ptilopachus* is placed in its own subfamily, Ptilopachinae, and New World genera are part of Odontophorinae (Bowie et al. 2013). Odontophoridae probably originated in Africa and fossil-calibrated molecular phylogenies indicate that Ptilopachinae and Odontophorinae diverged from one another during the Late Eocene, 36–40 MYA (Fig 3; Cohen et al. 2012, Hosner et al. 2015, Wang et al. 2016). Hosner et al. (2015) has argued that the most likely biogeographic scenario is that the divergence of *Ptilopachus* and New World quails occurred after an ancestral species colonized western North America from eastern Asia via the Bering Land Bridge, which connected the 2 continents during much of the Cenozoic Era (Hopkins 1959, Marincovich and Gladenkov 1999, Sanmartín et al. 2001). Climatic conditions in polar and subpolar regions of North America and Asia were warm enough to support the growth of forests during the early and mid-Cenozoic Era (Graham 2011, Sanmartín et al. 2001), which would have provided a dispersal corridor for ancestral species of New World quail. Similar colonization scenarios, supported by fossil and genetic data, have been proposed for other vertebrate taxa (Macey et al. 2006, Burbrink and Lawson 2007, Beard 2008, Guo et al. 2012, Li et al. 2015).

Most phylogenetic studies focused on the position of Odontophoridae within Galliformes, but relatively few have explored relationships among genera of New World quails. Holman's (1961) comparative analysis of skeletal anatomy and morphology remains the most complete phylogenetic study based on morphology. He concluded that New World quails consisted of 2 groups based on differences in the structure of the pelvis: the *Dendrortyx* group (*Dendrortyx, Oreortyx, Colinus, Philortyx,* and *Callipepla*) and the *Odontophorus* group (*Odontophorus, Dactylortyx, Cyrtonyx,* and *Rhynchortyx*).

Recent phylogenetic analyses based on mitochondrial DNA (Williford 2013) and multilocus data (Hosner et al. 2015) have largely upheld Holman's (1961) *Dendrortyx* and *Odontophorus* groups. The major discrepancies between molecular- and morphological-based phylogenies are the phylogenetic positions of *Dendrortyx, Oreortyx, Philortyx, Odontophorus,* and *Rhynchortyx* within Odontophoridae. The tawny-faced quail (*Rhynchortyx cinctus*) occupies a basal position and represents a sister clade to all of the other New World genera (Williford 2013, Hosner et al. 2015). Genetic data revealed that 1) the mountain quail is the most basal member of the *Dendrortyx* group; 2) the tree quails (*Dendrortyx* spp.) represent a sister clade to lineage composed of *Philortyx, Callipepla,* and *Colinus;* and 3) that *Callipepla* and *Colinus* are each other's closest relatives (Hosner et al. 2015). Divergence of New World quail genera took place during the Miocene between 25 and 5 MYA (Williford 2013, Hosner et al. 2015). During this time, North America experienced a cooling climate, increased mountain-building, contraction of tropical forests, and the expansion of savannas, grasslands, and deserts (Graham 2011). Speciation within *Cyrtonyx, Odontophorus, Dendrortyx, Callipepla,* and *Colinus* probably occurred between the mid-Miocene and early Pleistocene (15–1 MYA; Zink and Blackwell 1998, Hosner et al. 2015, Williford et al. 2016). The tawny-faced quail, wood-quails, and the crested bobwhite most likely colonized South America after the formation of the Isthmus of Panama (3 MYA) because of their poor flight capabilities (Williford 2013, Hosner et al. 2015, Williford et al. 2016).

PHYLOGEOGRAPHY

Phylogeography is the study of principles and processes that influence the evolution of geographic patterns of genetic variation (Avise 2000). Processes such as population expansion, range fragmentation, long-term isolation, and population bottlenecks produce characteristic geographical patterns of DNA polymorphisms. Therefore, phylogeographic studies aid in discerning the specific biogeographic events that shaped a species' geographic distribution. The phylogeography of a species in conjunction with historical climate data provide insight into how that species might respond to current or future events that could alter their geographic distribution. The phylogeographic structure of many animals and plants was heavily influenced by the climatic and environmental changes associated with Pleistocene glacial cycles (Avise 2000; Hewitt 2000, 2004; Maggs et al. 2008; Turchetto-Zolet et al. 2013). Complex phylogeographic patterns and deep genetic discontinuities among regional populations observed in North American and Eurasian taxa probably resulted from past isolation in separate refugia during the Last Glacial Maximum (19,000–26,500 yr ago). Weak or a complete lack of phylogeographic structure may be indicative of a population contraction into a single refugium (Avise 2000; Hewitt 2000, 2004; Soltis et al. 2006). Warm-temperate species of North America and Eurasia often display genetic signatures of postglacial expansion from refugia, including shallow mitochondrial phylogeographic structure, geographically widespread haplotypes, and high haplotype but low nucleotide diversity (Avise 2000; Hewitt 2000, 2004). Some cold-adapted mammals display genetic signals of rapid population decline (Galbreath et al. 2009, Campos et al. 2010, Palkopoulou et al. 2013), which underscores how rapidly species may be affected, negatively or positively, by changes in long-term weather or climate patterns. Contemporary climate change is particularly germane because it is a major factor in shifting distributions for a wide array of species (Walther et al. 2002). The most thorough phylogeographic studies of New World quails have been conducted on the bobwhites and the scaled, California, and Gambel's quails. The geographic distribution and phylogeographic structure of these quails has been heavily influenced by historical climate changes (Gutíerrez et al. 1983, Zink and Blackwell 1998, Williford 2013, Williford et al. 2016). Moreover, phylogeographic studies also provide a means of testing subspecies taxonomy based on physical traits such as coloration, plumage variation, and body size (Avise 2000, 2004).

The Bobwhites

The northern, black-throated (*Colinus nigrogularis*), and crested (*C. cristatus*) bobwhites occupy allopatric ranges, with the northern bobwhite distributed across the eastern United States and México; the black-throated bobwhite in scattered localities in the Yucatán Peninsula, Honduras, and Nicaragua; and the crested bobwhite in Central and South America to Brazil. These 3 species exhibit extensive geographic variation in male plumage throughout their respective ranges, which has led to the description of multiple subspecies. However, it is important to note that ornithologists disagree on the number of valid species and subspecies of bobwhite (Mayr and Short 1970, Madge and McGowan 2002, Dickerman 2007). Genetic data also confirmed the species status of the black-throated bobwhite and that the black-throated and northern bobwhites are more closely related to each other than to the crested bobwhite (Williford et al. 2016).

The northern bobwhite displays little phylogeographic structure overall, signals of relatively recent population expansion, and no congruence between patterns of genetic variation and subspecies taxonomy or biogeographic barriers (Eo et al. 2010; Miller 2014; Williford et al. 2014a, 2016). The lack of genetic differentiation among subspecies is observed even among the geographically isolated masked (*C. v. ridgwayi*) and Cuban (*C. v. cubanensis*) bobwhites (Williford et al. 2014a, 2016). Eo et al. (2010) argued that the signal of recent population expansion in northern bobwhites from the eastern United States resulted from demographic growth associated with European colonization, agriculture, and land clearance. However, the signals of population expansion observed in the northern bobwhite are also characteristic of species that underwent range expansion after the termination of the last Pleistocene glaciation (10,000 yr ago; Williford et al. 2014a, 2016). Post-Pleistocene expansion is also supported by ecological niche models of past and present geographic distributions for the northern bobwhite (Williford et al. 2016). The ecological niche models predict that the northern bobwhite's geographic range in the United States changed dramatically over the past 130,000 years in response to climatic oscillations, but remained comparatively stable in México (Williford et al. 2016). Ecological niche models also predicted a range contraction within the United States during the Last Interglacial (120,000–140,000 yr ago), a time when the Earth's climate was as much as 3° C warmer than present (Kukla et al. 2002). Continuous high summer temperatures negatively affect bobwhite populations by reducing the amount of usable space, length of the nesting season, percentage of nesting hens, and overall reproductive output (Klimstra and Roseberry 1975; Forrester et al. 1998; Guthery et al. 2001, 2005; Reyna and Burggren 2012). Warmer climates coupled with changes in precipitation and vegetation communities may have limited the distribution of the northern bobwhite in much of the United States during the Last Interglacial.

Phylogeographic structure was more pronounced in the black-throated and crested bobwhites than in the northern bobwhite (Williford et al. 2016). Populations of black-throated bobwhite in the Yucatán Peninsula are genetically differentiated from those in Nicaragua. This indicates that the most southerly subspecies, *Colinus nigrogularis segoviensis*, is a genetically distinct taxonomic unit; however, genetic data did not support the existence of 3 subspecies in the Yucatán Peninsula. The crested bobwhite exhibited the greatest amount of intraspecific genetic differentiation, and mitochondrial DNA phylogeography supported the existence of 3 or 4 distinct genetic groups. None of these groups were congruent with the current subspecies taxonomy, but may show some concordance with past or present biogeographic barriers. Some ornithologists have treated crested bobwhites in the northern portion of Central America (Guatemala to Costa Rica) as a separate species, the spot-bellied bobwhite (*C. leucopogon*), on the basis of geographic isolation and plumage variation (Peters 1934, Blake 1977, Johnsgard 1988, Madge and McGowan 2002); however, Williford et al. (2016) found no strong genetic evidence to support this view. Genetic data support the hypothesis that the ranges of the black-throated and crested bobwhite have been relatively stable since the end of the Pleistocene, but the results of ecological niche modeling suggested that both species experienced range expansions during the previous glacial period (Williford et al. 2016). The cooler, dryer conditions during the Last Glacial Maximum resulted in the fragmentation and contraction of tropical rainforests and the spread of more open habitats such as grasslands, savannas, and open woodlands in Central and South America (Hooghiemstra and van der Hammen 1998, van der Hammen and Hooghiemstra 2000, de Vivo and Carmignotto 2004). Ecological niche modeling also indicated that ranges of black-throated and crested bobwhites contracted during warm periods of the Mid-Holocene (6,000 yr ago) and the Last Interglacial, possible as a result of the expansion of tropical forests and the reduction of open habitats. As with the northern bobwhite, warmer temperatures during the breeding season may have negatively affected black-throated and crested bobwhites.

The incongruence between subspecies taxonomy and phylogeographic structure in bobwhites may be due to the often arbitrary and subjective nature of the phenotypic-based subspecies designations. Plumage differences may have evolved more recently after post-Pleistocene range fragmentation and isolation because nuclear genes associated with phenotypic traits may evolve at a different rate than mitochondrial genes. For example, Drake et al. (1999) found that masked bobwhites could be differentiated from captive northern bobwhites originating from wild populations in the United States using loci from the major histocompatibility complex. The major histocompatibility complex is involved in acquired immunity and is under intense selection pressure, which probably results in rapid evolution and differentiation among geographically isolated populations. Alternatively, plumage differences may be ancient but the signal of past isolation in mitochondrial DNA has been erased by secondary contact, admixture, or introgression (Williford et al. 2016).

Several geographically small-scale studies have found evidence for genetic differentiation among subspecies of the northern bobwhite (Nedbal et al. 1997, White et al. 2000, Halley et al. 2015). Nedbal et al. (1997) concluded substantial genetic differentiation between Texas (*C. virginianus texanus*) and the eastern bobwhite (*C. v. virginianus*) as part of a study of population restoration. White et al. (2000) found that masked and Texas bobwhites were more closely related than either was to populations from the eastern United States. Williford et al. (2014a) also found smaller genetic distances between masked and Texas bobwhites, but little differentiation within Texas. The discrepant conclusions may be attributed to geographic sampling and the genetic markers used. The White et al. (2000) sample size was relatively small and a limited number of populations were sampled. Nedbal et al. (1997) used 6 mitochondrial loci, which probably captured more accumulated genetic differences. Similarly, a recent study of bobwhites in Texas and Oklahoma based on whole mitochondrial genomes from 50 individuals revealed 2 divergent lineages separated by 103 mutational steps (Halley et al. 2015), but genetic differentiation was not congruent with subspecies, or ecoregions. Although the findings of Nedbal et al. (1997), Halley et al. (2015), and Williford et al. (2016) appear to be at odds, it should be noted that Williford et al. (2016) detected 3 mitochondrial lineages based on the analysis of the geographic distribution of genetic polymorphisms. One lineage was largely restricted to southern Texas and México, the second was most abundant in the United States, and a third rarer lineage occurred in scattered localities in México and the United States. It is possible that 2 of the weakly differentiated lineages detected by Williford et al. (2016) may be identical to genetic clusters identified by Nedbal et al. (1997) and Halley et al. (2015). The use of a single mitochondrial gene and a small number of nucleotides in several recent studies (Eo et al. 2010; Williford et al. 2014a, 2016) may provide only a weak phylogeographic signal, thus preventing or limiting the detection of genetic differentiation (Halley et al. 2015). In contrast, the results of studies that have used multiple mitochondrial loci (Nedbal et al. 1997, Halley et al. 2015) are difficult to interpret in a phylogeographic context because of the extremely limited sampling of the northern bobwhite's extensive geographic distribution. Future phylogeographic studies of the northern bobwhite should be conducted on a range-wide scale and use multiple mitochondrial and nuclear loci to gain an accurate understanding of this species' biogeographic and demographic history.

Other Species of New World Quails

The genus *Callipepla* consists of 4 species with partially overlapping geographic ranges distributed throughout much of southwestern North America. Elegant (*Callipepla douglasii*), California, and Gambel's quails were formerly placed in the genus *Lophortyx,* distinct from, but closely related, to the scaled quail (Holman 1961). Genetic data later supported relationships based on morphological data, and showed that these 4 species were each other's closest relatives (Gutíerrez 1993, Zink and Blackwell 1998). Zink and Blackwell (1998) were unable to resolve the phylogenetic position of the scaled or elegant quails relative to California and Gambel's quails, but recent multilocus data supported the hypothesis that *Callipepla* is divided into 2 sister clades: 1 composed of California and Gambel's quails and the other of elegant and scaled quails (Hosner et al. 2015).

The California quail was the first species of New World quail to be the focus of a phylogeographic study (Zink et al. 1987). Allozymic data revealed weak phylogeographic structure and genetic differentiation among the subspecies of California quail (Zink et al. 1987), a conclusion also supported by mitochondrial DNA sequences (Williford 2013). Zink et al. (1987) concluded that the geographic distribution of genetic variation supported the hypothesis that the California quail dispersed into Baja California after the peninsula's union with the southern California 3–5 MYA. Analysis of mitochondrial DNA sequences revealed that the scaled quail exhibits low genetic diversity, little phylogeographic structure, and evidence of postglacial demographic expansion (Williford et al. 2014b). Scaled quail displayed the greatest amount of genetic diversity in southern Texas, whereas genetic diversity was lower in the remainder of the scaled quail's geographic range. This suggests that southern Texas or northern México may have served as a refugium for the scaled quail during the Pleistocene, and the species expanded after the termination of the last major glaciation (Williford et al. 2014b).

The Gambel's quail exhibits strong phylogeographic structure, with divergent lineages separated by a large genetic gap (Williford et al. 2014c), unlike the northern bobwhite, scaled, and California quails. Many desert-adapted species in North America exhibit a phylogenetic break between populations in the Chihuahuan and Sonoran desert regions (Riddle and Hafner 2006). The geographic distribution of the 2 lineages of Gambel's quail was suggestive of a similar split, consistent with past fragmentation and isolation in separate refugia during the last glacial period (Williford et al. 2014c). The current geographic distributions of the 2 lineages overlap substantially, probably as a result of range expansion and secondary contact that occurred after the end of the Pleistocene.

Most subspecies of scaled, California, and Gambel's quails are based on minor variations of body size, and plumage coloration and tone (Madge and McGowan 2002). As with the bobwhites, phylogeographic studies of California, Gambel's, and scaled quails found little congruence between geographic patterns of genetic variation and subspecies taxonomy (Zink et al. 1987; Williford et al. 2014b, c). One possible exception to this was observed in the scaled quail. The chestnut-bellied scaled quail (*C. squamata castanogastris*), a subspecies restricted to southern Texas and northeastern México, exhibited weak but statistically significant genetic differentiation from scaled quail in the western part of the species' range (Williford et al. 2014b). Genetic diversity was also higher in the range of the chestnut-bellied scaled quail than in the western portion of the range. This may imply that southern Texas and northeastern México served as a Pleistocene refugium for scaled quail and that the scaled quail came to occupy much of its western range as a result of recent range expansion (Williford et al. 2014b). However, additional genetic markers and increased sampling will be necessary to confirm this finding.

Phylogeographic structure also appears to be weak in Montezuma quail. Allen (2003) found that Montezuma quail from Arizona and Texas were not genetically distinct from one another based on mitochondrial DNA sequences. One reason for this is that Montezuma quails in Arizona and Texas may not have been isolated from one another long enough to achieve significant genetic differentiation. The number of valid species of wood-quails (*Odontophorus* spp.) remains uncertain (Johnsgard 1988, Madge and McGowan 2002). Despite the use of mitochondrial and nuclear DNA sequences, Hosner et al. (2015) failed to resolve species relationships among the wood-quails but also found no support for plumage-based phylogenetic relationships proposed by Johnsgard (1988). The assessment of species limits among the wood-quails will probably require the use of not only multilocus data but broader taxonomic and geographic sampling and multivariate analysis of morphometric and plumage traits.

POPULATION AND LANDSCAPE GENETICS

Population genetics is the study of the genetic composition of populations, and specifically focuses on changes in allele frequencies and allelic diversity as a function of mutation, migration, genetic drift, and inbreeding (Gillespie 2004). Landscape genetics is the study of how contemporary landscape features and environmental gradients influence genetic structure at population and individual levels and affect evolutionary processes, such as gene flow and natural selection (Manel and Holderegger 2013). Collectively, population and landscape genetics provide insight into maintenance and loss of genetic diversity, adaptation to environmental changes, sex-biased dispersal, and rates of gene flow among populations (Gillespie 2004, Manel and Holderegger 2013).

The northern bobwhite has been the subject of most population and landscape genetics studies of New World quails. Early studies of bobwhite population genetics relied on allozymes (Ellsworth et al. 1988, 1989). As a result of the ease of sample preparation and their higher variability, microsatellite DNA markers (or short tandem repeats) have largely replaced allozymes as the most important marker for the study of contemporary population structure, genetic relatedness, dispersal, genetic drift, and population size changes in wild populations (DeYoung and Honeycutt 2005, Selkoe and Toonen 2006). The development of polymorphic microsatellite markers for the northern bobwhite (Schable et al. 2004, Faircloth et al. 2009) has resulted in a recent surge of population and landscape genetics studies. Research on the population and landscape genetics of other species of New World quails has been more limited although polymorphic microsatellite markers have been developed for the scaled quail (Orange et al. 2014), California and Gambel's quails (Gee et al. 2003), mountain quail (for the purposes of molecular sexing; Delehanty et al. 1995), and the black-breasted wood-quail (*Odontophorus leucolaemus;* Hale and Hughes 2003).

Population and Landscape Genetics of Northern Bobwhite

As with mitochondrial DNA, studies that used allozymes (Ellsworth et al. 1989) and microsatellites (Valentine 2007, Terhune 2008, Evans et al. 2012, Berkman et al. 2013a, Miller 2014) concluded that the northern bobwhite exhibits weak population structure. The weak genetic differentiation among bobwhite populations in the southeastern United States and the Great Plains is correlated with habitat fragmentation and dispersal barriers (Terhune 2008, Miller 2014). Populations of northern bobwhite in Illinois, in contrast, exhibit no correlation between genetic differentiation and potential dispersal barriers (Berkman et al. 2013a). Northern bobwhite populations in southern Texas also exhibit no correlation between genetic differentiation and dispersal barriers; but, unlike Illinois, populations do display weak signal of isolation by distance (Wehland 2006, Miller 2014). This may be due to the possibility that bobwhites are unlikely to disperse from favorable habitat (Berkman et al. 2013b) or, in the case of south Texas, the existence of sufficiently large areas of suitable habitat and few dispersal barriers (Miller 2014). Despite sharp, ongoing population declines and habitat fragmentation, most studies employing molecular markers have shown that genetic diversity in northern bobwhites is relatively high and similar among populations (Eo et al. 2010, Evans et al. 2012, Miller 2014, Williford et al. 2014a). Species characterized by short lifespans, high population turnover, and limited dispersal capabilities are expected to exhibit not only a high degree of population structure but also low or highly variable levels of genetic diversity (Harrison and Hastings 1996). Genetic effects of population fragmentation may be obscured by a number of confounding factors, including signals of past demographic expansions (Congdon et al. 2000) and historically large census and effective population sizes (Mbora and McPeek 2010). Mating system also influences effective population size, genetic diversity, and population structure (Wright 1965, Nunney 1993, Withler et al. 2004, Pearse and Anderson 2009). Mating systems that incorporate >1 male mate/female are likely to have higher effective population sizes (Sugg and Chesser 1994). Although usually described as monogamous, recent studies have revealed that northern bobwhites often engage in polygamy and polyandry (Curtis et al. 1993, Burger et al. 1995). Polygynous mating, the ability to produce 2 broods/year, and mixing of subpopulations via the autumn dispersal of juveniles may serve to maintain high genetic diversity and effective population size and overall weak population structure observed in northern bobwhites (Miller 2014). Finally, a species may undergo demographic collapse at such a rapid rate that it is driven to extinction before the negative impacts of low genetic diversity become apparent (Lande 1988). The demographic collapse that has occurred in many parts of the northern bobwhite's range may have occurred too rapidly to have had a noticeable impact on genetic diversity.

Genetic Consequences of Translocations of Wild and Pen-reared Northern Bobwhite

Attempts to restock or supplement declining bobwhite populations often involved the use of translocated wild or and pen-reared birds (Brennan 2007, Brennan et al. 2014). Hybridization and introgression between native populations and translocated or captive-bred stocks can erase historical genetic records, reduce genetic diversity, and lead to the loss of local adaptations (Rhymer and Simberloff 1996, Avise 2004, Champagnon et al. 2012). Aldrich (1946a, b) argued that lack of adaptation to local environments would prevent the long-term survival of bobwhite subspecific stocks introduced to regions outside of their natural ranges. If this reasoning is correct, the effects of interbreeding should have a limited effect on receiving populations. Several case studies of captive-bred bobwhites provide insightful inductions.

Most genetic studies of bobwhites have failed to detect introgression from translocated or captive-bred bobwhites (Valentine 2007; Berkman et al. 2013a; Williford et al. 2014a, 2016). As a result, captive-bred bobwhites seem to lack the behaviors necessary for survival in the wild (Roseberry et al. 1987, Hernández et al. 2006, Newman 2015). Overall, the results of field studies suggest that translocated wild and pen-reared bobwhites have lower rates of survival than native birds and fail to establish self-sustaining populations (Buechner 1950, Roseberry et al. 1987, DeVos and Speake 1995, Nedbal et al. 1997; but see Phillips 1928, Pitelka 1948, Evans et al. 2009, Woods 2013, Halley et al. 2015). This is perhaps because wild bobwhites typically have higher genetic diversity than do captive-bred stocks (Ellsworth et al. 1988, Evans et al. 2009).

Population Genetics in Other Species of New World Quails

Population genetics studies of *Callipepla* species have focused on the dynamics of natural hybridization between California and Gambel's quails in southern California. The geographic ranges of both species overlap, but the species differ in plumage and vocalization (Gee 2005, Gee et al. 2013, Calkins et al. 2014). Gee (2004) found a gradient of genetic, plumage, and morphometric traits highly correlated with a west-to-east gradient of environmental variables across the hybrid zone. Hybrids more closely resemble the California quail on the western side of the hybrid zone, whereas birds resembling the Gambel's quail become more common on the eastern side of the hybrid zone (Gee 2004). Fitness costs associated with interspecific hybridization may be outweighed in mixed species coveys by the fact that resident pairs, including mixed species pairs, begin breeding earlier than pairs that form outside of the covey (Gee 2003).

Wood-quails are unique among New World quails in that they live in small groups of 4–10 individuals year-round (Johnsgard 1988, Madge and McGowan 2002). The use of playback calls and microsatellite genetic analysis confirmed that the black-breasted wood-quail lives in groups consisting mostly of closely related adults and offspring that occupy the same territory for many years and defend it against conspecifics (Hale 2004, 2006). High levels of relatedness among juveniles within coveys suggested that monogamy may be the dominant mating strategy in black-breasted wood-quails (Hale 2004). Although genetic data indicated that coveys of black-breasted wood-quails were largely composed of close relatives, coveys also contained unrelated or distantly related individuals, which suggests that covey structure is not that of a simple nuclear family (Hale 2004). Hale (2004) also found that genetic relatedness and differentiation was negatively correlated with geographic distance for males but not females, which indicates that females may disperse from natal sites more often than males.

GENOMICS

The most common genetic markers, including most mitochondrial DNA or microsatellite loci, are selectively neutral. Therefore, the markers are useful for the estimation of relationships and recent demographic history among individuals, populations, or taxa, but are often blind to adaptive variation. Management units based solely on neutral variation may risk the loss of local adaptation (Bekessy et al. 2003, Hoekstra et al. 2004, Pérez-Emán et al. 2010). Population structure based on geographic patterns of neutral genetic variation may be congruent with the geographic distribution of diversity in genes related to adaptive traits. For example, the plumage-based subspecies taxonomy of the Central American passerine, the slate-throated redstart (*Myioborus miniatus*), is not congruent with the species' mitochondrial DNA phylogeographic structure despite experimental evidence that color patterns on the tail are instrumental in prey capture (Pérez-Emán et al. 2010). The widespread use of mitochondrial DNA and microsatellites has been due partly to the expense and difficulty of producing genetic markers, such as single nucleotide polymorphisms (SNPs), to assess adaptive variation (Avise 2004, DeYoung and Honeycutt 2005). In addition, genome resources for model organisms were lacking, and practically nonexistent for nonmodel organisms. However, recent technological advances, new sequencing technology, and increases in computing power have made the production of large numbers of SNPs from nonmodel organisms routine; rapid and cost-efficient assessment of population structure, genetic diversity, and adaptive variation is now a reality (Davey and Blaxter 2011, Ekblom and Galindo 2011). In fact, the cost of sequencing whole genomes has become less expensive and the number of whole genomes from nonmodel organisms is increasing rapidly (Dheilly et al. 2014, Ellegren 2014).

Rawat et al. (2010a, b) produced the first annotated library of genomic data for the northern bobwhite. The genomic library is available through the Bird Genomics Knowledge Base (http://systemsbiology.usm.edu/BirdGenomics/NBwhite_Transcripotmics.html; originally available the Quail Genomics Knowledgebase, http://www.quailgenomics.info). A draft genome for the northern bobwhite was completed in 2014 (Halley et al. 2014) and can be accessed through the publically available database GenBank (http://www.ncbi.nlm.nih.gov/). The genome is not yet annotated, but serves as a resource for SNP discovery and future discovery of adaptive variation.

FUTURE DIRECTIONS AND MANAGEMENT IMPLICATIONS

Little is known about the molecular ecology of most species of New World quail, including many species that are currently in decline. Range-wide phylogeographic studies of the wood-quails, tree-quails, tawny-faced, Montezuma, ocellated, singing, mountain, banded, and elegant quails are necessary to ascertain levels of genetic diversity and population structure—the first steps toward delineation of management units. Conclusions from previous studies regarding phylogeographic history, subspecies taxonomy, and management units within the northern, black-throated, and crested bobwhites and the California, Gambel's, and scaled quails should be confirmed using different markers and methodologies. For example, an ideal future range-wide phylogeographic study of the 3 bobwhite species would incorporate whole mitochondrial genomes, and SNPs or whole nuclear genomes, sampled over a broad geographic range. Transcriptome research on the northern bobwhite is necessary in order to fully annotate the bobwhite genome and increase its usefulness. The continuing decrease in cost and difficulty of conducting genomic research on non-model organisms will allow quail biologists to more easily assess adaptive variation in wild populations.

Genetic data have shown that morphology-based subspecies may not always be an accurate guide to the geographic distribution of genetic diversity. Therefore, assessment of genetic distinctiveness should be carried out before using subspecies as management units. Phylogeographic studies combining genetic data and ecological niche modeling have shown that all 3 bobwhite species are highly sensitive to past climatic oscillations. All 3 species exhibited contractions during the last major glaciation and during the last interglacial, when the Earth's climate was much warmer. Other species of New World quails may be equally sensitive to climatic fluctuations. Incorporating future climate change into the management of New World quails will require the use of molecular methods and ecological niche modeling to gain insight into how these species responded to past climatic changes and to identify regions that served as refugia during warm and cold periods.

Despite the pressing need for additional ecological research on both well-studied and relatively unknown species, molecular genetics have provided us with new insights about the biology of wild quail that are of interest and value to managers. In the northern bobwhite, for example, dispersal and connectivity are apparently a much more important factor driving population structure than originally thought. This finding then leads to the implication that the scale of our management efforts should be extended from individual properties to the broader landscape or even ecological region.

Molecular genetics, when used in conjunction with other tools such as ecological niche modeling (Williford et al. 2016), provides managers with an objective basis for understanding why these birds are found where they currently exist, at least at the scale of their geographic distribution. Such information points to the folly of efforts to translocate species outside of their native ranges, which has been tried for many different species of quails over many years. If managers and other stakeholders considered the evolutionary factors that shaped the geographic distributions of quails that we observe today, they would see that efforts to translocate California quail from California to Pennsylvania (proposed back in the 1990s), or to translocate California quail from eastern Oregon to East Texas (an active proposal at the time of this writing, believe it or not) are likely to be wastes of time and treasure. In contrast, using the translocation to successfully recolonize restored habitats, as has been done with mountain quail in southeastern Oregon (Budeau and Hiller 2012), represents the evolutionary basis of a management success.

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STRATEGIC HABITAT CONSERVATION FOR DECLINING GRASSLAND WILDLIFE POPULATIONS IN THE OAKS AND PRAIRIES JOINT VENTURE

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ABSTRACT

Degradation and conversion of functioning grassland ecosystems in North America has driven significant declines in grassland wildlife populations across multiple taxa. In an effort to address declines in the grasslands of Oklahoma and Texas, a number of governmental agencies and Non-Governmental Organizations have partnered to form the Oaks and Prairies Joint Venture (OPJV) to more strategically and collaboratively deliver conservation actions in this region. With northern bobwhite (*Colinus virginianus*) as the flagship species, OPJV has worked to implement a fully integrated Strategic Habitat Conservation framework that works at multiple scales to conduct biological planning, landscape conservation design, habitat tracking and population monitoring in support of conservation efforts aimed at restoring not just northern bobwhite, but a variety of bird and pollinator species that depend on healthy grasslands. The signature conservation delivery program of this effort was the Grassland Restoration Incentive Program (GRIP) which has improved habitat for grassland wildlife on over 24,300 hectares of working lands in focus areas throughout the OPJV geography since it was created in 2013. The Grassland Restoration Incentive Program was accompanied by a full complement of conservation delivery programs that support prescribed burning associations and other landowner cooperatives, utilize market-based conservation delivery strategies, and implement strategic outreach and communications. The conservation efforts were supported by over 4,500 point counts annually in National Bobwhite Conservation Initiative Coordination Implementation Program focal areas as well as 7 focal regions, each comprising clusters of 2-8 counties. Combining the efforts of multiple partners ties the range-wide population and habitat objectives with on-the-ground conservation actions for quail, other grassland birds, butterflies, and grassland pollinators.

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Key words: *Colinus virginianus*, habitat management, northern bobwhite, partners, Joint Venture, population objective, grassland birds

INTRODUCTION

Degradation and conversion of functioning grassland ecosystems in North America has driven significant declines in grassland wildlife populations across multiple taxa. Habitat loss and fragmentation were considered primary causes of the range-wide decline in northern bobwhites (Brennan 1991, Williams et al. 2004, Hernandez et al. 2013), and many other grassland and shrub-grassland associated bird species (Brennan and Kuvlesky 2005). More conservation groups are starting to recognize the need for landscape-scale conservation, and that landscape-scale conservation will require cooperation of government agencies, non-governmental organizations, universities, and individual landowners working together to meet the landscape-level conservation challenges.

Williams et al. (2004) suggested effective conservation of northern bobwhite populations would require "scaling up management of habitat." They further stated, "Managers must explicitly prioritize usable habitat availability and conservation and develop regionally based joint-venture partnerships for efficient delivery of

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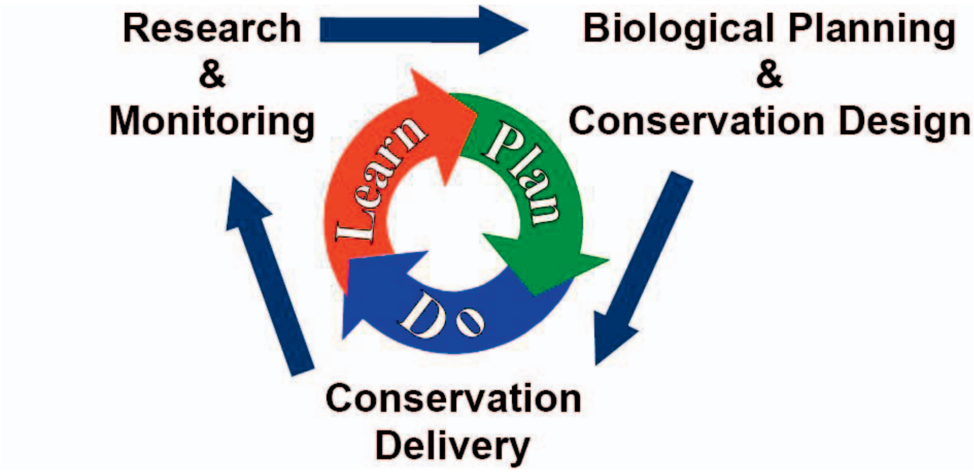

Fig. 1. Strategic Habitat Conservation includes biological planning, conservation design, conservation delivery, and research and monitoring in a Plan-Do-Learn cycle to address uncertainties in a continuous cycle. All activities require communications of relevant information to appropriate audiences.

management regimes (Pg. 867).” They continued, “…we should promote development of regional joint ventures (through local conservation cooperatives that join local residents and both nongovernmental and governmental agencies) in which partners work together toward an appreciation of landscape relationships…” Our purpose was to describe Bird Habitat Joint Ventures (JVs) in general and identify Joint Ventures with significant responsibility to conserve northern bobwhites. Then we describe how the Oaks and Prairies Joint Venture partners are working together to “scale up management of habitat” as a case study of a Joint Venture focusing on grassland conservation for priority bird populations.

Bird Habitat Joint Ventures and Northern Bobwhite Populations

Bird Habitat Joint Ventures (JVs) are “regional, self-directed partnerships of government and non-governmental organizations as well as individuals working across administrative boundaries to deliver landscape-level planning and science-based conservation, linking on-the-ground management with national population goals (Giocomo et al. 2012).” The 18 U.S. Bird Habitat Joint Ventures work to implement national and international bird conservation plans, as well as other state and species conservation plans such as the National Bobwhite Conservation Initiative (NBCI) (National Bobwhite Technical Committee 2012). In general, Joint Ventures bring together local and regional partner agencies and organizations, who, in many cases, are already separately delivering conservation actions on the ground, to build support systems that allow for national and regional planning (landscape-scale) to inform local conservation action decisions, while local habitat, socio-economic, and bird population conditions inform landscape-scale planning and programs.

JVs work under an adaptive management framework developed by the US Fish and Wildlife Service and US Geological Survey known as Strategic Habitat Conservation (NEAT 2006). Under this adaptive management framework, activities can be broken into biological planning, conservation design, conservation delivery, assumption-based research, mission-based monitoring, and communications (Figure 1). Each activity feeds information into the next activity in a cycle that eventually (usually every 5-10 years) leads to a new cycle of biological planning informed by the previous cycle. Each JV partnership decides which species and activities to prioritize in the adaptive management framework. The broad scope and diversity of habitat needs for hundreds of bird species at different times of the year (breeding season, migration, and wintering) requires this adaptive approach which recognizes that significant knowledge gaps exist.

Partners in Flight (PIF), a national landbird conservation cooperative, conducted an analysis of landbird populations based upon Breeding Bird Survey data. For northern bobwhites, PIF identified at least 10 of the 18 United States (US) Bird Habitat JVs with significant populations of the northern bobwhites (>1% of the estimated world population; Rosenberg et al. 2016). All populations showed decreasing long-term and short-term trends (Rosenberg et al. 2016; Table 1). Several of these JVs are working on elements of the adaptive management framework to address conservation needs of northern bobwhites in particular and grassland birds in general, and some have made significant progress.

Oaks and Prairies Joint Venture Partnership

In 2008, the Texas Parks and Wildlife Department and the Oklahoma Department of Wildlife Conservation partnered with federal government agencies and non-governmental organizations (NGO) to form the Oaks and Prairies Joint Venture (OPJV) to more strategically and collaboratively deliver conservation actions in central Oklahoma and Texas. A major goal of the OPJV was the maintenance, improvement, or restoration of breeding, wintering, and resident grassland bird populations and the

Table 1. Joint Ventures with significant populations of northern bobwhites (> 1% of the world population) and their Brid Conservation Regions (BCR). Included are long-term (decline 1966-2013 according to the Breeding Bird Survey) and short term trend (average annual trend from 2003-2013 from Breeding Bird Survey) (Rosenberg et al. 2016).

Joint Venture	BCR	Northern Bobwhite Area Importance	Long-term trend	Short-term Annual Trend
Appalachian Mountains	28	1%	-98%	-6.9%
Central Hardwoods	24	7%	-86%	-5.1%
East Gulf Coast	27	5%	-91%	-5.3%
Gulf Coast	37	2%	-79%	-3.3%
Lower Mississippi Valley	25, 26	4%	-92%	-5.8%
Oaks and Prairies	20, 21	8%	-93%	-7.3%
Playa Lakes	18, 19	23%	-28%	-5.4%
Rain Water Basin	19	2%	-35%	-4.7%
Rio Grande	35, 36	8%	-59%	-2.1%
Upper Mississippi River & Great Lakes	22, 24	17%	-79%	-5.4%

habitat(s) on which they depend. The OPJV used a Strategic Habitat Conservation framework integrated horizontally at the ecoregional scale to conduct biological planning, conservation design, conservation delivery, monitoring (habitat and population), research, and, communications, to vertically link field scale conservation actions and research with national and state level biological planning, monitoring, and conservation delivery efforts (Table 2).

OPJV partner organizations collaborated on the development of a set of biological objectives (e.g., threats, priority species, population estimates, population objectives, habitat objectives derived from species-habitat models) which were meant to provide a shared purpose to guide strategic decision-making (biological planning). These objectives were lofty, explicit, and based on the best available science and population models to answer questions such as: “how large are the current bird populations?”; “how many more are needed to meet shared desired population levels?”; “how much more habitat is needed to support the desired future populations?”

Early in the development of the OPJV, partners identified habitat loss and alteration due to changes in land use and natural disturbance processes as major drivers of population declines. These changes included altered fire cycles, livestock grazing practices, brush encroachment, use of non-native forages and crops, and urban/suburban development (Oaks and Prairies Joint Venture 2007). Working with partner staff land managers, biologists, university researchers, and other scientists, OPJV partners identified a set of grassland priority species that ranged from grassland specialist like grasshopper sparrow (*Ammodramus savannarum*) and eastern meadowlark (*Sturnella magna*), to shrubland specialist like painted bunting (*Passerina ciris*) and Bell’s vireo (*Vireo bellii*), to more generalist species like northern bobwhite.

Initial habitat objectives were derived by calculating the population loss over the most recent decade at the time of planning for the Oaks and Prairies Bird Conservation Region (BCR) for each of the priority species. Using population estimates from the PIF Population Estimates Database (Partners in Flight Science Committee 2013) as a starting point, and subtracting estimated population loss for declining species using Breeding Bird Survey trend (2001-2011; Sauer et al. 2012), we were able to calculate the number of territories needed to add to the population in the next 10-years to maintain the population assuming population loss in the next decade was going follow the same trend from the last decade. The number of territories was then multiplied by a species specific average territory size obtained from published literature values to calculate a minimum habitat objective. We assumed territories represented “ideal” habitat conditions for each species and the area of habitat needed was a minimum estimate because there can be space left unused in a seemingly suitable habitat patch.

For example, the northern bobwhite population estimate for the Oaks and Prairies BCR was 345,000 territories, with a 10-year population loss of 38% resulting in a loss of 131,100 territories. Using an average territory size of 6.7 ha based upon literature review and expert opinion, we calculated a minimum area of new usable space needed, or habitat objective of $131{,}100 * 6.7 = 878{,}370$ ha. We assumed species with similar habitat needs could be represented by the same habitat acres, and maximum habitat needs for grassland specialists and shrub specialists combined represented the OPJV habitat objective for the next 10 years. In the case of the OPJV geography, the 10-year goal was for an additional 5% of the 24.2 million ha geography (1.2 million ha habitat objective) to provide usable space for grassland and grass/shrub birds such as northern bobwhite.

The overall OPJV population-based habitat objective served three purposes. It provided and estimate of the overall scale of the need for conservation (e.g., 4,000 ha vs. 400,000 ha of conservation actions per year). It provided a benchmark to measure the annual rate of progress toward an overall goal. Finally, the population-based habitat objective served as a reality check to keep the conservation programs to create and restore habitat tied to the priority bird populations, instead of the conservation programs themselves becoming the focus of partner attention.

Table 2. Strategic Habitat Conservation activities at spatial scales ranging from national to individual fields managed by private landowners with partner technical guidance, including example partners and programs. Gray items indicate main areas of concentration for Oaks and Prairies Joint Venture (OPJV) activities to link National Planning with field level conservation action. (NBCI – National Bobwhite Conservation Initiative, NRCS- Natural Resources Conservation Service, RCPP- Regional Conservation Partnership Program, EQIP- Environmental Quality Incentives Program, TPWD- Texas Parks and Wildlife Department, ODWC- Oklahoma Department of Wildlife Conservation, FSA CRP- Farm Service Agency Conservation Reserve Program, FWS- Fish and Wildlife Service, LIP- Landowner incentive program, QF-Quail Forever).

		Vertical Dimensions - Activity					
		Biological Planning	**Conservation Design**	**Conservation Delivery**	**Monitoring**	**Research**	**Communications**
Horizontal Dimensions - Spatial Scale	**National**	NBCI and Partners in Flight		NRCS RCPP	Breeding Bird Survey		
	State	State Wildlife Action Plans, TPWD, ODWC		NRCS EQIP, FSA CRP, FWS Partners Program, TPWD LIP	Breeding Bird Survey, State Agency Fall Counts		
	Joint Venture/ Ecoregion	Implementation Plan/Technical Team Plans	JV Conservation Planning	OPJV Grassland Restoration Incentive Program	Breeding Bird Survey		OPJV Communication Strategy
	Focus Area (clusters of counties)			OPJV Grassland Restoration Incentive Program	OPJV Grassland Bird Monitoring	OPJV Human Dimensions	OPJV Communication Strategy
	County			NRCS EQIP, FSA	OPJV Grassland Bird Monitoring	OPJV Human Dimensions	Agricultural Extension
	Field			NRCS District Conservationist, TPWD Technical Guidance Biologists, ODWC Private Lands Biologists, and QF Farm Bill Biologists working with Private Landowners	Citizen Science (e.g., landowner quail surveys, eBird)	University Research Projects	

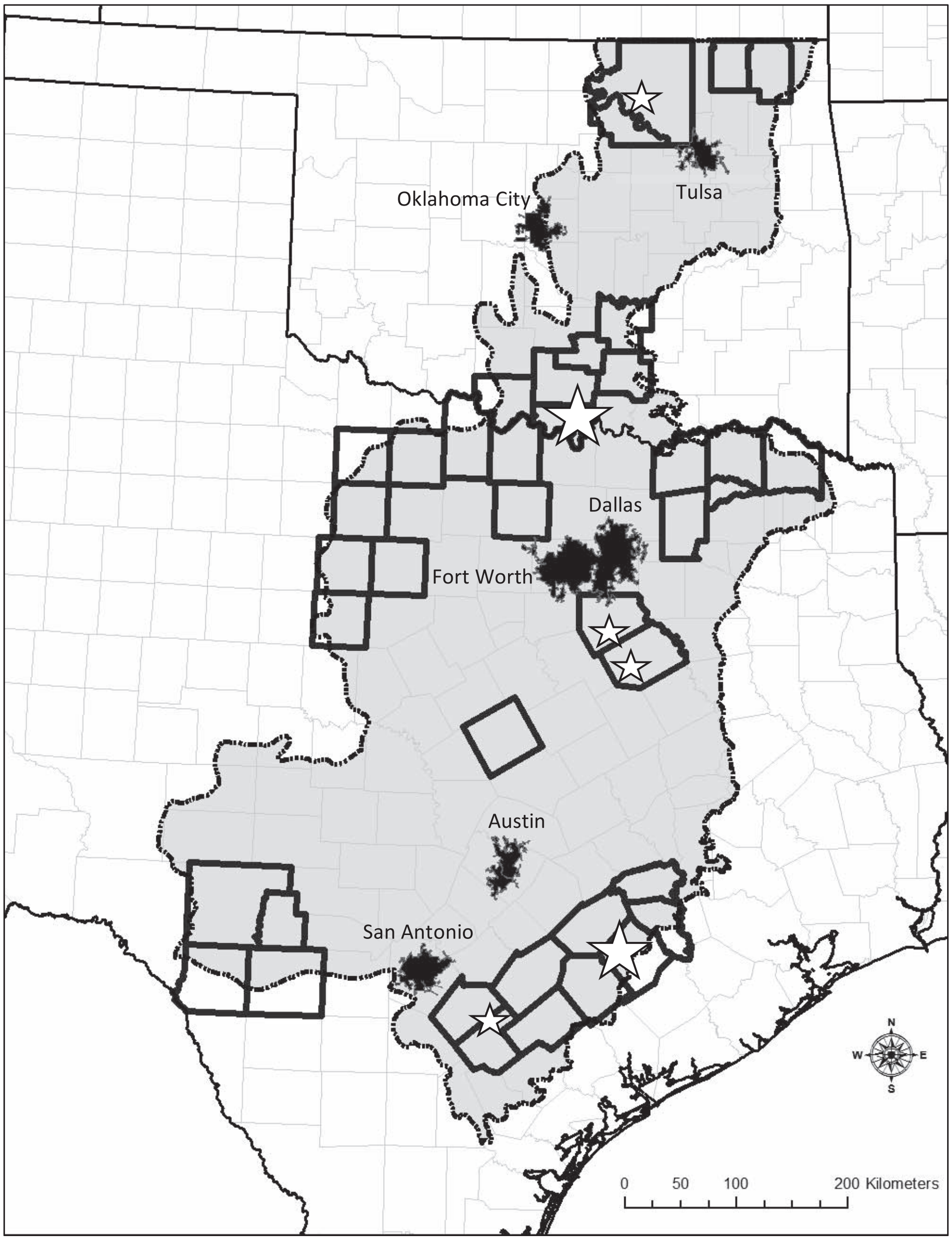

Fig. 2. Focal regions is the Oaks and Prairies Joint Venture region (gray) include 30 counties in Texas and 10 counties in Oklahoma (black outlined counties). Large stars indicate "official" National Bobwhite Conservation Initiative (NBCI) Coordinated Implementation Program focal areas in Colorado County, TX and Love County, OK. Small stars indicate additional focal areas with breeding season monitoring reported by Texas and Oklahoma state agencies in the NBCI habitat management inventory.

Once biological objectives were identified, OPJV partners began assessing the conservation potential of the landscape and providing spatially-explicit locations for conservation activities (conservation design). This process was intended to answer questions about "Where does grassland habitat exist?", "Where are the most cost effective locations for conservation?", and "Where should conservation actions be focused?" Our partners decided to use counties as the planning unit for the OPJV. Clusters of counties to serve as focus areas (Figure 2) for partner investment toward shared grassland conservation goals were selected based upon priority bird range maps, partner interest, and the NBCI Biologist Ranking Information (National Bobwhite Technical Committee 2012). Within some of the clusters of counties, smaller focus areas (sub-county), including the Texas and Oklahoma NBCI focal areas, were established around conservation activity hotspots, including existing wildlife or prescribed fire landowner cooperatives. These county clusters (OPJV focus areas) and sub-county focus areas served as areas for concentrated partner cooperation for our monitoring and conservation delivery efforts (see below for OPJV Grassland Bird Business Plan).

OPJV monitoring efforts consist of bird population monitoring and conservation tracking of habitat management. The bird population monitoring was designed to be a long-term (10-year) distance sampling using roadside point counts for several priority grassland birds during the breeding season, including northern bobwhite. The bird population monitoring was also designed to supplement national and state bird monitoring (e.g., Breeding Bird Survey and fall covey call counts) at the county scale to match the scale of our biological planning, conservation design, and conservation delivery. Several universities and state agencies, including Texas Parks and Wildlife Department, Oklahoma Department of Wildlife Conservation, Texas State University, and Oklahoma State University, were involved in funding, conducting, and logistically supporting monitoring efforts (over 4,500 point counts per year), increasing shared ownership of the monitoring effort.

Conservation tracking efforts within the OPJV partnership attempted to count and map acres managed to support grassland bird conservation efforts. Oaks and Prairies Joint Venture and partner staff collected habitat data before and after habitat improvement projects were completed and logged the data collected into a shared online database called the Grassland Management Inventory Tool. Combined, these two monitoring efforts helped the JV partners to evaluate progress toward achieving conservation goals and longer-term population response to landscape management. Ultimately, population monitoring and conservation tracking can provide needed information to justify conservation practices and programs while producing information to improve future conservation planning in the adaptive management cycle (Giocomo et al. 2012).

Cooperative research efforts could provide an opportunity to address uncertainties in assumptions used for biological planning and conservation design. Working under the adaptive management framework, replicated blocks of managed and unmanaged habitat could be identified to test basic assumptions built into our conservation strategy. The most basic assumption was that our priority species population will respond to large-scale habitat management. Large-scale test of basic assumptions have not been initiated in the Oaks and Prairies, but several small research projects are in progress to evaluate northern bobwhite survival and productivity in areas where our conservation delivery has been concentrated. For example, one project initiated by partners at Tarleton State University in Texas was following radio-marked northern bobwhites in GRIP project areas and surrounding control areas to evaluate the effects of prescribed fire on demographic parameters.

Finally, better understanding of the human dimensions of grassland conservation including studies of social, political, and economic conservation drivers, needed to be incorporated into all other activities under the adaptive management framework at different scales. The OPJV partners began a pilot project in one of our focus areas using public data (e.g. US Census Bureau) and GRIP participant data to attempt to build predictive models for landowner participation in conservation programs. We also developed strategic communication strategies (e.g. targeted landowner workshops, websites, and publications) to reach specific audiences, including individual landowners, land managers, and cooperative quail conservation groups, and surveys to evaluate the effectiveness of those communication tools to cause desired behavioral outcomes (Bogart et al. 2009, Giocomo et al. 2012).

OPJV Grassland Bird Conservation Business Plan and GRIP

Recognizing the complexity and difficulty of restoring grassland bird populations across a large geography of private working lands, the OPJV partners enlisted a full complement of conservation delivery strategies. The OPJV Grassland Bird Conservation Business Plan (Oaks and Prairies Joint Venture 2015) was our main tool to communicate identified the delivery strategies and to estimate costs, risks, and potential contribution to habitat objectives for each strategy. Business plan strategies were implemented through programs made available at the landscape level and delivered locally by OPJV partners, including: financial incentives to private landowners for habitat management, support of landowner conservation cooperatives , market-based conservation delivery, and strategic outreach and communications.

The portfolio of programs employed balanced risk (likelihood of success) by including both innovative approaches that are less proven but have a high potential for conservation gain, with more traditional approaches that have a demonstrated history of success in making modest conservation gains. An example of a more traditional conservation strategy identified in the plan, and implemented by the OPJV partners, was to provide financial incentives for private landowners to conduct habitat management practices on their property through the OPJV Grassland Restoration Incentive Program (detailed below).

An example of a higher risk conservation strategy was to develop an incubator for nascent landowner cooperative groups to develop organizational capacity to identify and pursue conservation resources and communicate successes. Support could be things as simple as helping to develop stable leadership and bylaws, providing website development support, and providing information and contacts for various conservation programs provided by partner agencies and organizations. Although success is not guaranteed, the landowner cooperative groups fostered by this program have the potential to deliver large conservation gains and serve as a force multiplier for efforts to conduct conservation outreach in the OPJV geography. This strategy has not been fully implemented yet in the OPJV.

The OPJV partners implemented GRIP in 2013 to be delivered in parallel with the US Department of Agriculture Natural Resource Conservation Service's (NRCS) Environmental Quality Incentive Program (EQIP) in order to address missed opportunities for conservation projects on private lands due to eligibility issues or landowner reluctance to work with the federal government. The program was delivered locally by Texas Parks and Wildlife Department, NRCS, US Fish and Wildlife Service, or other partner organization staff. The practices that were incentivized through the program were a subset of the practices incentivized through EQIP and could be categorized into 4 main categories; brush management, native grass reseeding, prescribed burning, and prescribed grazing. Practices incentivized by GRIP were all selected by experts who identified them as the most effective means of improving grassland bird habitat.

Using northern bobwhite as a flagship species, GRIP has been able to deliver a little over $1.1 million dollars in direct funding for habitat improvements. This spending has resulted in over 24,300 ha of improved habitat at a cost to the program of under $20 per acre. The functional unit for decision-making for GRIP exists at the focus area scale where local initiative teams made up of agency staff met regularly to discuss GRIP practices, policies and procedures in order to ensure that program dollars are having the greatest impact possible on target bird species.

Funding for GRIP came from various sources (federal, state, and private), but regardless of source, funds were administered by OPJV partner NGOs thereby easing complications that often accompany government contracting. Demand for GRIP consistently exceeded partner expectations and funding availability. We believe that NGO administration was the primary reason that GRIP was received so favorably by landowners and local resource professionals delivering the program.

As successful as GRIP was in gaining interest from landowners thereby facilitating private land habitat improvements, implementing GRIP also identified challenges for our ability to achieve landscape level population objectives. Aside from the obvious needs for increased and more reliable funding as well as increased conservation delivery capacity, it was also apparent that financial incentive programs may only be effective tools for a subset of landowners in a given area. In order to win the battle for the "hearts and minds" of landowners in the OPJV who exhibit diverse motivations and management approaches, it will be necessary to offer an equally diverse set of strategies to encourage conservation action to scale-up management.

CONCLUSION

The Oaks and Prairies Joint Venture partnership is continuing to build upon previous grassland conservation efforts, and join together efforts across scales, agencies, organizations, and species to address grassland habitat needs for northern bobwhites, grassland birds and other grassland species as well as individual private landowners and public land managers. Through our partnership's application of Strategic Habitat Conservation efforts over the past decade, our biological planning and conservation design helped to guide our initial conservation efforts through the Grassland Restoration Incentive Program supported by over 40 partner organizations. The OPJV has delivered habitat gains by working with partners committed to northern bobwhite and grassland bird conservation. Since 2013, over 24,300 hectares (60,000 acres) of GRIP conservation practices were supported by over 10,000 bird point counts monitoring efforts through 2016. This effort was the first half of our 10-year plan. With planning, conservation delivery, monitoring, and communications efforts happening at the same time, in the same places, and at the same (county) scale, we were able to leverage partner efforts with the NRCS Regional Conservation Partnership Program (U.S. Farm Bill Program) to scale up habitat management resources and staffing to meet the landowner demand, demonstrated through our partner supported GRIP efforts, through 2021.

More than half of the JVs in the United States have significant responsibility for northern bobwhite populations, and may provide avenues for less traditional conservation measures to address conservation needs for grassland birds. There are also emerging opportunities to combine efforts for other steeply declining grassland dependent species to bridge the traditional divide between game and non-game species. Scaling up of grassland habitat management requires combining the efforts of multiple partners to tie range-wide population and habitat planning efforts with local-scale, on-the-ground conservation actions for northern bobwhite, other grassland birds, butterflies, and grassland pollinators. To make significant progress against seemingly overwhelming conservation challenges, we will need to be willing to tie together different strategies and work across different scales with many partners.

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TEMPORAL AND SPATIAL ASSESSMENT OF USABLE SPACE AND COVER TYPE INTERSPERSION FOR NORTHERN BOBWHITES ON PRIVATE FARMLANDS IN SOUTHWESTERN OHIO

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ABSTRACT

Contemporary landscape change driven by socio-economic forces and advances in agricultural technology do not favor northern bobwhites (*Colinus virginianus*) in the Midwestern United States. The challenge of bobwhite conservation is to provide sufficient quantities of habitat with optimal configurations in proportions that satisfy needs throughout the year on private-owned working lands. We radio-tracked 58 coveys and 98 individual birds throughout the year in 2009-10 and 2010-11 on privately owned farmland in southwestern Ohio. We investigated temporal changes in usable space from use-availability data. Estimated proportions of usable space based on analyses of habitat selection across four study sites were 0.06-0.12 during the non-breeding season compared to 0.10-10.30 during the breeding season. We also modeled probabilities that radio-marked coveys or individual birds used points within individual cover types as a function of distance to other cover types. Locations of radio-marked coveys and individual birds within focal cover types were closer to other cover types compared to random points during breeding (mean = 44 m) and non-breeding (mean = 58 m) seasons. Probability of use within focal cover types declined with distance to other cover types, typically falling below 50% when distances exceeded 9-242 m. Locations of radio-marked coveys were concentrated near edges within used cover types, while locations of individual birds were more dispersed during the breeding season. Estimated proportions of usable space based on distances between locations of radio-marked bobwhites and nearest cover types were higher (0.30-0.53) than estimates based on habitat selection ratios, and were similar between non-breeding and breeding seasons. Potentially usable sites were not fully occupied in either season, but there was no relationship between crude covey densities and proportions of usable space estimated from habitat selection analyses during the breeding and non-breeding seasons across study sites and years ($r^2 < 0.166$, $P > 0.316$). With distance to cover type estimates of usable space (years combined), two study sites with the highest proportions of usable space (0.43-0.53) also had the largest crude covey densities (0.0065-0.153 coveys/ha) compared to the other two sites with lower proportions of usable space (0.30-0.32) and smaller covey densities ($0.004 - 0.006$ coveys/ha). Habitat enhancement should focus on providing protective cover near food for coveys during the non-breeding season and protective cover near nesting and brood-rearing habitat during the breeding season. Conserving Midwestern bobwhite populations requires innovative practices that can be implemented on private lands as economic incentives change for farm operators. Improving protective cover along habitat edges can increase usable space by improving cover type juxtaposition (e.g. food near cover) while minimizing impact on farming practices.

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Key words: *Colinus virginianus*, habitat use, interspersion, northern bobwhite, Ohio, private lands, quail, radio-telemetry, usable space

In contrast to migratory bird populations where conservation is delivered within discrete ecoregions to address limiting factors during separate stages of the annual life cycle (i.e. wintering, breeding, and migration), conservation planning for resident game bird populations such as northern bobwhite (*Colinus virginianus*; hereafter bobwhite) must efficiently allocate scarce resources to meet focal species' needs throughout their annual life cycle within the same landscape. Managers of resident bird populations must provide sufficient amounts of habitats in optimal proportions that satisfy needs during

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breeding and non-breeding seasons. Bobwhites are exceptionally challenging in this regard as they are a prototypical edge species with small seasonal home ranges and thrive in fine-grained landscapes (Roseberry and Sudkamp 1998).

Landscape change driven mostly by socio-economic forces, advances in agricultural technology, and urbanization do not favor bobwhites (Brennan 1991, Williams et al. 2004). Diversity and interspersion of cover types that satisfy food, cover, and other life requisites has declined and populations are increasingly isolated as the Midwestern landscape becomes more simplified and coarse-grained. Some habitats are over-supplied (e.g. croplands) while others are under-supplied (e.g. nesting and protective cover types) which limits the capacity of a focal area to support bobwhite populations. Although capable of relatively long-distance dispersal during fall and spring "shuffles" (Liberati 2012, Smith 2015), bobwhites are vulnerable to predation when they move long distances between food and protective cover during winter, resulting in unsustainably low over-winter survival (Janke and Gates 2012, Gates et al. 2012).

Given the challenge of managing habitat for bobwhites throughout the year and the potential sensitivities of population growth to vital rates during limiting stages of the annual life cycle, (Folk et al. 2007, Sandercock et al. 2008, Gates et al. 2012), conservation planning can be informed by quantifying the capacity of an area to support bobwhites with knowledge of use, availability, and proximity of cover types. Guthery (1997) proposed the concept of usable space for northern bobwhite habitat assessment and management, shifting the focus of management and conservation away from individual landscape elements (i.e. food plots or discrete cover patches) and toward an emphasis on the composite suitability of a focal area. Addition of a time dimension allows a dynamic representation of how much of a focal area is usable for bobwhites at a given time within the constraints of "physical, behavioral, and physiological adaptations" of bobwhites (Guthery 1997: 294). Guthery et al. (2005) provided a method for temporal quantification of usable space from habitat use-availability data, providing the opportunity to identify periods of the annual life cycle when habitat might be most limiting.

Guthery's (1997) conception of usable space applies habitat selection coefficients from habitat use-availability data to areas of cover types within a focal area. Some cover types may be used in proportions less than available because they are overabundant on the landscape relative to what a species needs. Alternatively some cover types may have low use due to suboptimal interspersion and juxtaposition or because they lack suitable vegetation structure and composition (Wiley 2012). Usable space considers the quality of an entire area rather than quality of cover types within an area (Guthery 1997). Usable space estimates better represent use of space than home range estimators by reducing the influence of areas with minimal or no use (Hiller et al. 2009). Dividing abundance by usable space provides estimates of ecological density that are generally more informative than crude density (Roseberry and Klimstra 1984, Guthery 1997).

The usable space concept considers seasonal variation in resource requirements and availability (Guthery 1997). For instance, a row crop field may not provide food or cover during nesting, but can be important during brood rearing and winter (Janke and Gates 2012, Liberati and Gates 2017, *in review*). Temporal variation in usable space could affect seasonal demographic parameters (e.g. reproduction and survival) that determine population growth rates (Folk et al. 2007, Sandercock et al. 2008, Gates et al. 2012). Combined with demographic data and estimates of ecological density, seasonal quantifications of usable space can identify periods when habitat is limiting and thereby inform efforts to improve the quality of a given area.

The Guthery et al. (2005) method of estimating usable space does not explicitly consider spatial distribution of cover types as a potential constraint on habitat use. Use of particular cover types is influenced by distance to surrounding cover types (Leopold 1933, Schroeder 1985). Fragmented habitats may have patches that are too isolated to be usable (Thomas and Taylor 2006). Spatial variation in use of cover types should be considered along with relative use of different cover types when applying the usable space concept. Together, these two approaches provide spatially and temporally explicit representations of suitability of a focal area for bobwhites, and prepare managers with information they need to make decisions about habitat management and restoration. We applied Guthery's (1997) concept of usable space to understand how availability and configuration of cover types affected capacities of four study sites with different habitat composition and configuration of land cover to support bobwhite populations throughout the year. Our objectives were to; 1) estimate usable space from habitat use-availability data 2) determine effects of cover type proximity on usable space during breeding and non-breeding seasons; and 3) compare usable space between breeding and non-breeding seasons. We illustrate an approach to target habitat conservation designed to address landscape- and regional-level limiting factors on private lands in the Midwestern United States.

STUDY AREA

Our study was conducted on four private land sites centered at 39° 04′59″, 83° 39′10″ in Highland and Brown Counties in southwestern Ohio (Figure 1) in the glaciated till plains physiographic region of Ohio (Ohio Division of Geologic Survey 1998). The Fee area was the most intensively-farmed study site, with relatively high proportions of row crop and low proportions of forest, early successional (ES) herbaceous, ES woody, and pasture/hay (Table 1). In contrast, the Wildcat and Peach Orchard study sites contained the largest proportions of ES herbaceous and woody cover types. Wildcat differed from Peach Orchard with a lower proportion of forest and more pasture/hay. The Thurner site had intermediate proportions of row crop, forest, and early successional

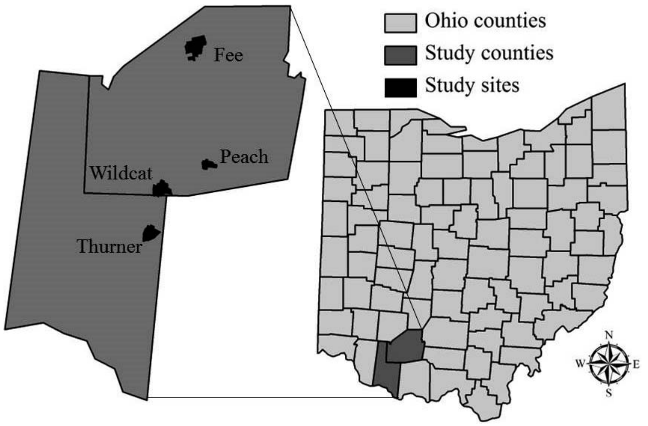

Fig. 1. Locations of four private land study sites where use of microhabitat and space by northern bobwhites was investigated in southwestern Ohio during 2009-2011.

cover types, but had the highest proportion of the ES woody cover type among all four study sites. Changes in cover type composition between years were largely due to adjustments of study area boundaries. The long-term (30 year) mean temperature during October-March was 10.5^{0} C. The long-term mean annual snow accumulation was 67.5 cm and accumulation during 2009-10 and 2010-11 was 101.6 cm and 67.3 cm, respectively (National Climate Data Center 2011).

METHODS

Cover Mapping

We manually digitized ground-truthed cover maps of each study site in ArcGIS (version 9.3, ESRI Redlands, CA, USA) over high spatial resolution (0.305 m, acquisition date 2007) ortho-photographs (Ohio Statewide Imagery Program 2008) as described in Janke and Gates (2013). Contiguous cover types within and adjacent to study site boundaries were classified into six cover types; row crop, forest, ES herbaceous, ES woody, pasture/hay, and non-habitat. Early successional herbaceous included CRP or old-fields, fencerows, ditches, and odd areas dominated by grasses and forbs. Early successional woody comprised fencerows, ditches, old-fields, or portions of CRP fields where shrubs dominated. Pasture/hay included fields actively grazed or hayed during the study. Conservation Reserve Program fields that were mowed to low heights (e.g. mid-contract management) were included in pasture/hay since they were structurally more similar to that cover type. Areas >50 m width and dominated by mature trees were classified as forest, while areas <50 m width and dominated by a dense shrubby understory were classified as ES woody. The row crop cover type included corn (*Zea maize*), soybean (*Glycine max*), and winter wheat (*Triticum aestivum*) fields and mowed grass-ways within crop fields. Non-habitat included residential and commercial properties, roads and associated ditches, and water. Site boundaries varied among years depending on access granted by landowners and included only areas that were thoroughly searched to find coveys during the non-breeding season.

Capture and Radio-marking

We used covey call surveys and systematic searches with pointing dogs to locate coveys on each study site before 1 December in 2009 and 2010. Snow tracking or periodic dog searches continued within areas not occupied by radio-marked coveys during 1 December – 28 February 2009-11. We captured bobwhites with baited funnel traps (Stoddard 1931) and targeted mist netting (Wiley et al. 2012). Capture efforts continued throughout the year to maintain ≥ 1 radio-marked bird per covey during winter and to deploy radio-transmitters on additional bobwhites during the breeding season. Captured bobwhites were leg-banded and most were radio-marked with pendant-style mortality-sensing radio-transmitters (6.6 g; Advanced Telemetry Systems, Isanti, MN, USA) if they weighed ≥ 165 g. Bobwhites were released at capture sites immediately after marking. We obtained daily locations of radio-marked birds over 6-7 days each week during the non-breeding season (Oct-Mar) using homing from short distances (White and Garrott 1990). Birds that remained alive after covey break-up were tracked as individuals throughout the breeding season (Apr-Sep). We tracked 98 previously and newly radio-marked bobwhites after covey break-up and through the end of the breeding season (Apr-Sep). We used a global positioning system to mark covey locations and recorded the cover type where birds were found. Trapping,

Table 1. Cover types available to northern bobwhites on four study sites in southwestern Ohio, 2009-2011.

		Percent of Cover Type					
Study Site	Year	Row Crop	Forest	ES[a] Herbaceous	ES[a] Woody	Pasture/Hay	Other
Fee	2009-10	76.1	6.6	6.9	2.9	3.3	4.2
	2010-11	72.1	8.3	9.1	3.1	3.3	4.1
Peach	2009-10	41.5	30.9	19.5	3.7	0.0	4.4
	2010-11	39.7	28.6	21.0	4.7	2.0	4.1
Thurner	2009-10	52.3	16.2	10.1	6.2	8.0	7.2
	2010-11	53.5	16.1	9.9	6.5	6.6	7.4
Wildcat	2009-10	40.6	9.6	22.4	4.2	19.3	3.9
	2010-11	38.5	10.4	19.6	4.2	23.3	4.0

[a] ES = early successional

handling, and marking protocols were reviewed and approved by the Animal Care and Use Committee at The Ohio State University (protocol number 2007A0228).

Temporal Analysis of Usable Space

We used Guthery et al.'s (2005) method to estimate the quantity of usable space based on monthly use-availability data. We determined proportional use (p_i) and proportional availability (a_i) on each study site by cover type (i). Letting $u_i =$ the unknown proportion of usable space within cover type i and $A_i =$ the area (ha) of cover type i, we estimated usable space (U) according to Guthery et al.'s (2005) definition

$$U = \sum_{i=1}^{w} u_i A_i,$$

where $w =$ the number of cover types available ($i = 1, 2, \ldots, w$).

With the assumption that coveys or individuals distribute themselves randomly throughout all usable space, we expected that;

$$p_i = u_i A_i / U,$$

which implied that;

$$U_i = u_i A_i / p_i.$$

Since U and $\mathrm{u_i}$ are both unknown, we used the selection ratio (p_i/a_i; (Manly and McDonald 1993) to estimate u_i within each cover type. We first assumed that the cover type (m), with the highest monthly selection ratio was fully usable ($u_m = 1$). Interestingly under this assumption, total usable space across all habitats could simply be calculated with the following formula;

$$U_m = A_m / p_m.$$

However, to determine individual contributions of cover types to total usable space, the u_i for cover types other than m ($u_{i'}$) must be relativized to the selection ratio of the most preferred cover type (u_m) by dividing the selection ratio of cover type i by the selection ratio of cover type m as follows;

$$u_{i'} = u_i / u_{m.}$$

Given that A_i was measured without error and the assumption that $u_m = 1$ was without error, Guthery et al. (2005) concluded that variance can be estimated as

$$\mathrm{var}(U) = (A_m)^2 * (1 - p_m)/(np_m)^3$$

We determined U within cover type i (U_i) as the product of u_i and A_i. Monthly estimates of usable space provided a temporal analysis of usable space.

Habitat selection ratios were derived from compositional analyses reported from Janke and Gates (2013) and Liberati and Gates (2017, *in review*). We estimated usable space by years and study sites and by month with years pooled across study sites. We calculated ecological densities of coveys on each site using site-specific area estimates of usable space during the non-breeding season.

Distance to Cover Types

We used telemetry locations from radio-marked coveys (non-breeding season) or individual birds (breeding season) to estimate distances from points that were used by bobwhites within cover types (hereafter "focal cover type", excluding non-habitat) to each of four cover types nearest to the focal cover type (hereafter "nearest other cover type"). Radio-locations were pooled across years within the four study sites during non-breeding and breeding seasons. The same numbers of random points were selected as the numbers of radio-locations recorded in each cover type within sites and seasons. These points were used as pseudo-absence points in logistic regression analyses. Coordinates of radio-locations and random points were overlaid on cover maps in ArcGIS. Euclidean distances (m) were calculated between each radio-location or random point in the focal cover type and all nearest other cover types. Some of the distances to nearest cover type were not distances to focal cover type edges, as distances were sometimes measured to nearest other cover types that did not contact focal cover types.

We used logistic regression in Program R version 3.2.2 (R Development Core Team 2015) to estimate probability of use of random points within focal cover types as a function of distance to the nearest other cover types. We started with models for each focal cover type that included the main effects of distances to other nearest cover types and all combinations of 2-way interactions that included the main effects. We used stepwise selection with Akaike's information criterion (AIC) to select a single model for each cover type during breeding and non-breeding seasons. We presented standardized parameter estimates for ease of interpretation but we plotted probabilities of use of points within focal cover types as a function of unstandardized distances to other cover types. Distances from radio-location points to other cover types were allowed to vary over ranges that we observed with distance to other cover types held at their means.

Spatial Analysis of Usable Space

We overlaid a 50 m x 50 m grid of points on cover maps of each study site and applied the predict function in program R to estimate probability of use of grid points within each focal cover type based on logistic regression parameters from the best-fitting models identified by stepwise selection. We interpolated a continuous probability surface of predicted use by bobwhites from probability values of the 50 m grid using the kriging function with cell size = 15 m in the Spatial Analyst extension of ArcGIS 10.0. The 15 m resolution of the kriging response surface corresponded with accuracy (12.9 m) of our radio-locations (Janke 2011). The response surface provided spatial representations of usable space based on proximity of adjacent cover types for each study site during breeding and non-breeding seasons.

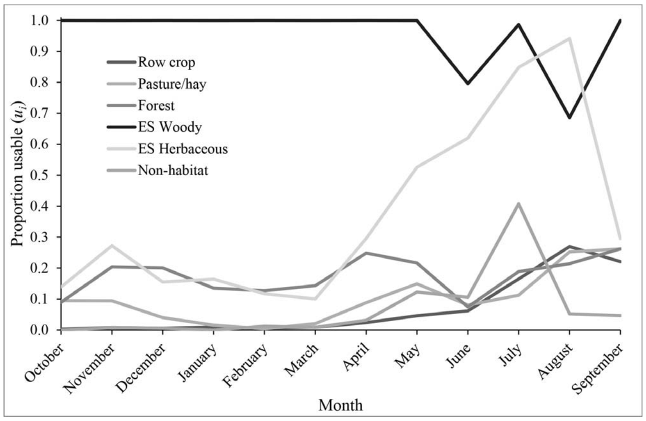

Fig. 2. Mean monthly estimates of proportional usable space within six cover types (u_i) based on radio-locations ($n = 3{,}664$ in 2009-10; $n = 4{,}636$ in 2010-11) of northern bobwhites in southwestern Ohio during 2009-2011 (years and study sites combined).

RESULTS

Temporal Analysis of Usable Space

We used radio-locations from 26 coveys ($n = 1{,}858$) and 51 individual birds ($n = 1{,}836$) to estimate usable space during breeding and non-breeding seasons in 2009-10. Equivalent numbers of radio-locations were recorded from 32 coveys ($n = 2{,}532$) and 47 individual birds ($n = 2{,}104$) and during non-breeding and breeding seasons in 2010-11.

The ES woody cover type had the highest selection ratios (p_i/a_i) of all cover types, ranging from 1.0 to 9.3 during the breeding season and from 8.5 to 16.6 during the non-breeding season (Appendices 1-4). Early successional herbaceous had the second highest selection ratios, ranging from 0.4 to 4.2 during the breeding season and from 0.8 to 3.1 during the non-breeding season. Selection ratios for forest ranged from 1.0 to 2.4 during April and May in 2010, in all months except for August during the breeding season in 2011, and all months except October 2009-10 during the non-breeding season. Selection ratios of row crop and pasture/hay were <1.0 in both seasons except during August 2010 and June 2011. Early successional woody was considered fully usable except during June-August 2010 when ES herbaceous had the highest selection ratio (Appendices 1-4).

Averaging proportional usability (hereafter u_i) across years, ES woody dominated all other cover types throughout the non-breeding season (Figure 2). However, u_i of ES herbaceous rose from 0.10 in March to 0.94 in August before falling to 0.3 in September. Similarly, u_i of row crop and pasture/hay increased from ≤ 0.02 in March to 0.22–0.27 in August and September. The usability proportion for forest varied monthly between 0.08 and 0.26 with no apparent seasonal pattern. Interestingly, u_i of non-habitat peaked at 0.41 in July when radio-marked bobwhites were sometimes found in road right-of-ways, raising the selection ratio of non-habitat to near 1.0 (Tables 2–3).

The ES woody cover type had the highest proportional use and was also the least abundant cover type on our study sites (Table 1). Conversely, row crop was the most abundant cover type but received low use relative to its availability. Consequently, small proportions (0.18 during 2009-10 and 0.13 during 2010-11) of our study sites were usable with estimates of usable space averaged across all months and study sites. Estimated proportions of usable space varied among study sites with months combined (Table 2). Thurner had the highest proportion of usable space (0.22), followed by Peach (0.15), Wildcat (0.13), and Fee (0.10).

Mean monthly proportions of usable space ranged from 0.06 - 0.12 during the non-breeding (Oct-Mar) season, to 0.11 to 0.36 during the breeding season (Apr-Sep) with study sites combined (Figure 3). The increase in proportion of usable space between non-breeding and breeding seasons corresponded with a large increase in proportional use of the ES herbaceous cover type, and smaller increases in proportional usability of row crop and pasture/hay during the breeding season (Figure 2). Proportions of usable space increased between non-breeding and breeding seasons on all four study sites. Seasonal variation in proportions of usable space was relatively consistent among study sites between years, although the increase in usable space between non-breeding and breeding seasons occurred much earlier during 2009-10 than in 2010-11 (Figure 3).

Crude covey densities were 1.4 -2.0 times higher on Wildcat compared to the other three study sites, although the Wildcat site ranked third in proportion of usable space

Table 2. Estimates of usable space and densities of northern bobwhite coveys by study site, year, and season in southwestern Ohio during 2009-2011.

			Usable Space (ha)			Covey Density/ha	
Study Site	Year	Total Area (ha)	Non-breeding	Breeding	No. Coveys	Total Area	Usable Space
Fee	2009-10	1106.7	72.7	168.3	7	0.0063	0.0963
	2010-11	1284.3	102.1	145.8	6	0.0047	0.0588
Peach	2009-10	310.2	17.1	92.5	2	0.0065	0.1170
	2010-11	397.7	36.4	55.4	1	0.0025	0.0275
Thurner	2009-10	593.7	126.7	176.7	3	0.0050	0.0237
	2010-11	738.8	120.7	154.3	6	0.0081	0.0497
Wildcat	2009-10	675.9	52.2	166.1	11	0.0163	0.2107
	2010-11	838.3	65.6	111.6	12	0.0143	0.1829

Table 3. Differences (use – random) of median distances (m) between northern bobwhite radiolocations and random points between focal and nearest other cover types during breeding (Apr-Sep) and non-breeding (Oct-Mar) seasons, 2009-2011 (years combined) in southwestern Ohio.

		Nearest Other Cover Type					
Focal Cover Type	Season	ES Herbaceous	ES Woody	Forest	Row Crop	Pasture/Hay	Row Mean
ES Herbaceous	Breeding		-4	76	-29	-61	-5
ES Woody	Breeding	-46		102	-3	-100	-12
Forest	Breeding	-120	-41		-14	-98	-68
Row Crop	Breeding	-180	-47	38		-155	-86
Pasture/Hay	Breeding	-87	-17	-50	-43		-49
Column Mean	Breeding	-108	-27	42	-22	-104	-44
ES Herbaceous	Non-Breeding		-46	0	-72	-77	-49
ES Woody	Non-Breeding	-29		32	-5	-96	-25
Forest	Non-Breeding	-104	-58		-23	-108	-73
Row Crop	Non-Breeding	-158	-92	-29		-115	-99
Pasture/Hay	Non-Breeding	-48	-44	-38	-49		-45
Column Mean	Non-Breeding	-85	-60	-9	-37	-99	-58

(Table 2). Consequently, ecological density (no. coveys/ha usable space) was highest on Wildcat, followed by Fee, Peach Orchard, and Thurner. There was no relationship between numbers of coveys and areas of usable space during the breeding ($r^2 = 0.166$, $P = 0.316$) and non-breeding seasons ($r^2 = 0.008$, $P = 0.837$) when covey densities were regressed on usable space estimates for each year and study site.

Distance to Cover Types

Frequency distributions of distances from radiolocations and random points to nearest other cover types were naturally right-skewed since negative distances were not possible. Therefore, we examined median distances to nearest cover types for used and random points. Median distances from radiolocations recorded in focal cover types were 25 m closer to other cover types than random points for 13 of 20 differences during the breeding season and 16 of 20 differences during the non-breeding season (Table 3).

We summarized differences (used - random) in median distances between used and random points for all pairs of cover types (Table 3). The resulting matrix was not symmetric so averaging differences across rows versus across columns produced different marginal means. The row marginal means summarized differences in distances between used and random points, averaged across nearest other cover types for each focal cover type. The column marginal means summarized differences in distances between used and random points averaged across focal cover types for each nearest other cover type.

Differences in distances between used and random points were more strongly negative when averaged across nearest other cover types within the forest, row crop, and pasture/hay focal cover types than for ES herbaceous and ES Woody focal cover types during the breeding and non-breeding seasons (row marginal means, Table 3). Differences in distances between used and random points were most strongly negative when averaged across focal cover types for the ES herbaceous, ES woody, and pasture/hay nearest other cover types during both the breeding and non-breeding seasons (column marginal means, Table 3).

Relative distances of used versus random points within the ES herbaceous and ES woody focal cover types varied among nearest other cover types during the breeding season (Table 3). Radio-marked bobwhites were closest to the pasture/hay cover types and were more distant from the forest cover type compared to random points when they occupied ES herbaceous and ES woody cover types. Bobwhites also were closest to ES herbaceous or pasture/hay within focal forest, row crop, and pasture/hay focal cover types during the breeding season.

Relative distances of used versus random points within focal cover types were consistently negative across all nearest other cover types except forest during the non-breeding season (Table 3). Radio-marked bobwhites were closest to ES woody, row crop, and pasture/hay cover types when they occupied the ES herbaceous cover type, and were closest to the ES herbaceous and pasture/hay cover types within the ES woody focal cover type during the non-breeding season. Bobwhites were closest to ES herbaceous, ES woody, or pasture/hay cover types when

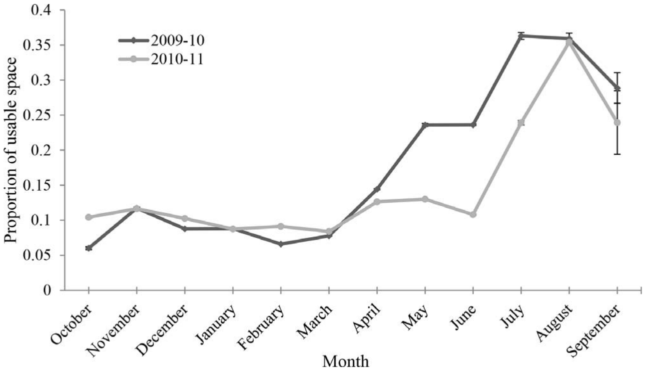

Fig. 3. Monthly trends in mean proportions of usable space by year for northern bobwhites in southwestern Ohio during 2009-11 (study sites combined). Error bars represent 95% confidence intervals.

Table 4. Mean predicted probability of use by northern bobwhites of 50 × 50 m grid points based on stepwise-selected logistic regression models of distance from focal to other nearest cover types. Grid points were distributed throughout four study sites in southwestern Ohio to generate predicted probability of use surfaces for each study site during non-breeding and breading seasons during 2009-2011.

			Breeding		Non-breeding		
Site	Cover Type	n[a]	Mean	SD	Mean	SD	P[b]
Fee	ES herbaceous	473	0.50	0.15	0.45	0.19	<0.0001
	ES Woody	162	0.41	0.23	0.39	0.19	0.1737
	Forest	417	0.29	0.25	0.33	0.27	<0.0001
	Pasture/hay	3710	0.27	0.26	0.25	0.25	0.2418
	Row Crop	175	0.27	0.22	0.29	0.23	<0.0001
	Total Area	4937	0.30	0.23	0.31	0.23	<0.0001
Peach	ES herbaceous	337	0.39	0.09	0.33	0.20	<0.0001
	ES Woody	70	0.28	0.18	0.35	0.17	<0.0001
	Forest	454	0.21	0.24	0.19	0.23	<0.0001
	Pasture/hay	28	0.66	0.11	0.59	0.14	0.0004
	Row Crop	647	0.34	0.25	0.36	0.24	0.0175
	Total Area	1536	0.32	0.23	0.30	0.24	0.0039
Thurner	ES herbaceous	296	0.46	0.08	0.46	0.23	0.7222
	ES Woody	202	0.39	0.18	0.46	0.14	<0.0001
	Forest	472	0.38	0.27	0.40	0.28	0.0001
	Pasture/hay	191	0.46	0.22	0.33	0.24	<0.0001
	Row Crop	1565	0.46	0.20	0.45	0.20	0.0362
	Total Area	2726	0.44	0.21	0.43	0.22	0.0417
Wildcat	ES herbaceous	663	0.49	0.10	0.40	0.22	<0.0001
	ES Woody	137	0.54	0.17	0.56	0.12	0.0226
	Forest	350	0.52	0.22	0.50	0.25	0.0002
	Pasture/hay	762	0.41	0.23	0.33	0.26	<0.0001
	Row Crop	1318	0.63	0.15	0.53	0.22	<0.0001
	Total Area	3230	0.53	0.20	0.45	0.24	<0.0001

[a] Number of grid points.

[b] Paired t-test.

they occupied forest, row crop, and pasture/hay cover types during the non-breeding season.

We evaluated 10 models that predicted probability of use of points within focal cover types as a function of distance to other cover types. We excluded non-habitat from analyses because this cover type received <1.0% use by radio-marked individuals or coveys during 16 of 24 months over 2 years and use never exceeded 8% in any month/year (Table 4). Stepwise selection retained all main effects of distance to cover types on use of points within ES woody, ES herbaceous, row crop, pasture/hay, and forest cover types (Appendices 5-6). Three to 5 of 10 possible 2-way interactions were retained after stepwise selection. Logistic regression coefficients on the log odds-ratio scale were negative for 16 of 20 main effects during the breeding season and 17 of 20 main effects during the non-breeding season. Interaction terms were significant ($P < 0.05$) for 15 of 18 retained interactions during the breeding season and 16 of 19 retained interactions during the non-breeding season (Appendices 5-6).

When graphed on the probability scale with all but one main effect held at their means, probabilities of use for 5 focal cover types declined with distance in 16 of 20 instances during the breeding season, and for 17 of 20 instances during the non-breeding season (Figures 4–8). Predicted probability of use of ES herbaceous cover was <0.50 and did not change with distance to ES woody during the breeding season and was >0.50 within 55 m of ES woody during the non-breeding season (Figure 4). Predicted probability of use of ES herbaceous was >0.50 within 75-81 m of row crop in each season. The probabilities of use for ES woody was >0.50 within 71-102 m from ES herbaceous, 14-31 m from row crop, and 129-237 m from pasture/hay during breeding and non-breeding seasons (Figure 5). Predicted probabilities of use for ES herbaceous and ES woody increased or changed very little with distance to forest and pasture/hay. Predicted probability of use for forest was >0.5 within 62-81 m of ES herbaceous cover, within 9-33 m of row crop, and within 110-112 m of pasture/hay (Figure 6).

Probability of use for forest was <0.5 at all distances to the ES woody cover type. Predicted probability of use for row crop was >0.5 within 170-217 m of ES herbaceous cover, within 37-60 m of ES woody cover, and within 203-242 m of pasture/hay during breeding and non-breeding seasons (Figure 7). Probability of use for row crop either increased or was <0.50 over nearly the entire range of distances to forest cover. Predicted probability of use for pasture/hay was >0.5 within 80-129 m of ES herbaceous cover and within 30-55 m of row crop during breeding and non-breeding seasons (Figure 8). Probability of use for pasture hay was <0.5 except within 29 m of ES woody and within 34 m of forest cover during the non-breeding season. Predicted probability of use for pasture/hay was <0.50 at all distances to the ES woody and forest cover types during the breeding season.

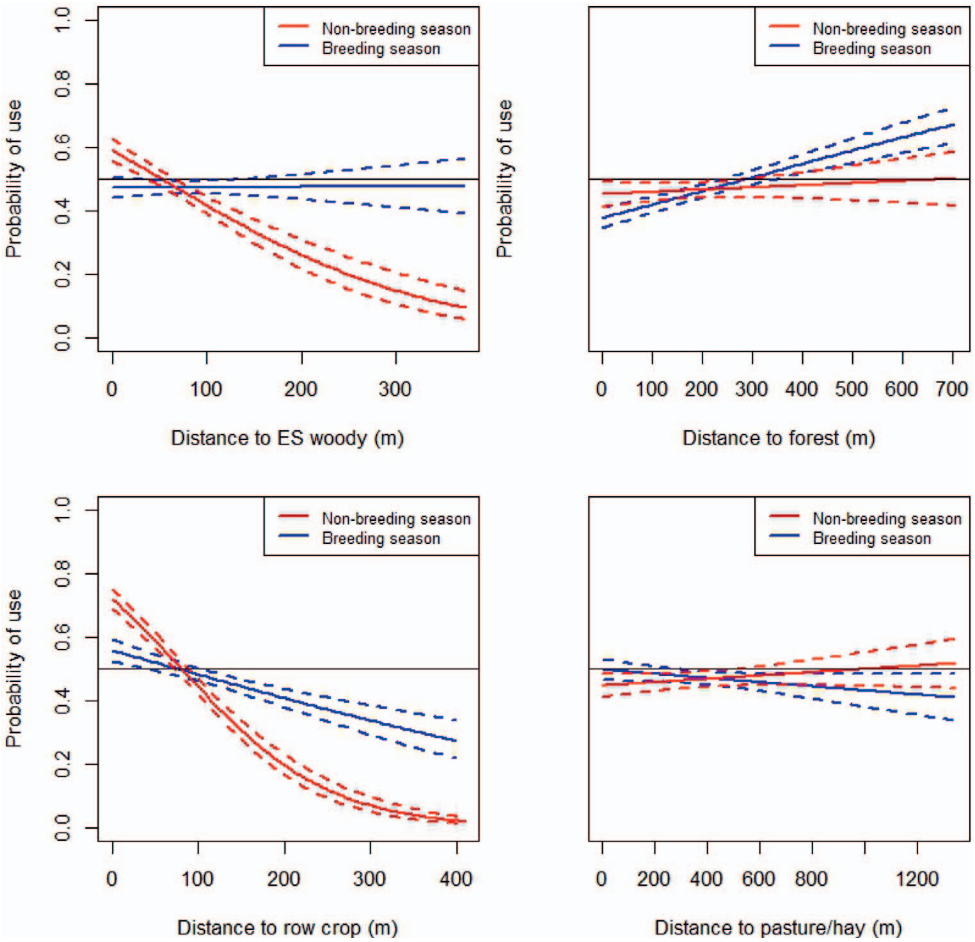

Fig. 4. Influence of distance to cover types on predicted probability of northern bobwhite use within the early successional herbaceous cover type in southwestern Ohio (years and study sites combined). Dashed horizontal curves represent 95% confidence intervals. The horizontal line represents the 0.50 threshold of predicted probability of use.

Spatial Analysis of Usable Space

Mean probabilities of use predicted from distances to nearest cover types during the breeding and non-breeding seasons were lower on the Fee and Peach Orchard sites than on the Thurner and Wildcat sites when aggregated across cover types (Table 4). There were small differences in predicted probabilities of use between breeding and non-breeding seasons for all but the Wildcat site, where aggregate probability of use was higher during the breeding season compared to the non-breeding season.

With relatively large *n*-sizes, we readily detected statistically significant differences in predicted probability of use of cover types within sites between the breeding and non-breeding seasons (Table 4) but the largest difference was 0.10 and we did not consider differences <0.05 as biologically relevant. Applying these criteria, ES herbaceous had higher predicted probability of use during the breeding season compared to the non-breeding season on all sites except Thurner (Table 4). ES woody had higher probability of use during the nonbreeding season compared to the breeding season on the Peach Orchard and Thurner sites. Pasture/hay had higher probability of use during the breeding season compared to the nonbreeding season on all sites except Fee. Row crop had higher predicted probability of use during the breeding season than during the non-breeding season on the Wildcat site, while predicted probabilities of use for forest did not differ between seasons at any site.

Different patterns of variation in predicted probabilities of use among cover types were observed on our four study sites (Table 4). Predicted probability of use was highest for ES herbaceous and ES woody compared to forest, row crop, and pasture/hay on the Fee site, while probability of use was substantially higher than other cover types on the Peach Orchard site. Mean probabilities of use were more consistent among cover types on the Thurner and Wildcat sites compared to the Fee and Peach Orchard sites. Since the same distance to cover type relationships were applied to grid points on each site, differences in predicted probabilities of use were caused by spatial arrangements of cover types that varied among study sites.

The row-wise differences in distances for used versus random points from focal to nearest other cover types (Table 3) summarized the distributions of radiolocations overlain on cover types (Figures 9–12). Radio-locations were concentrated near habitat edges within high use

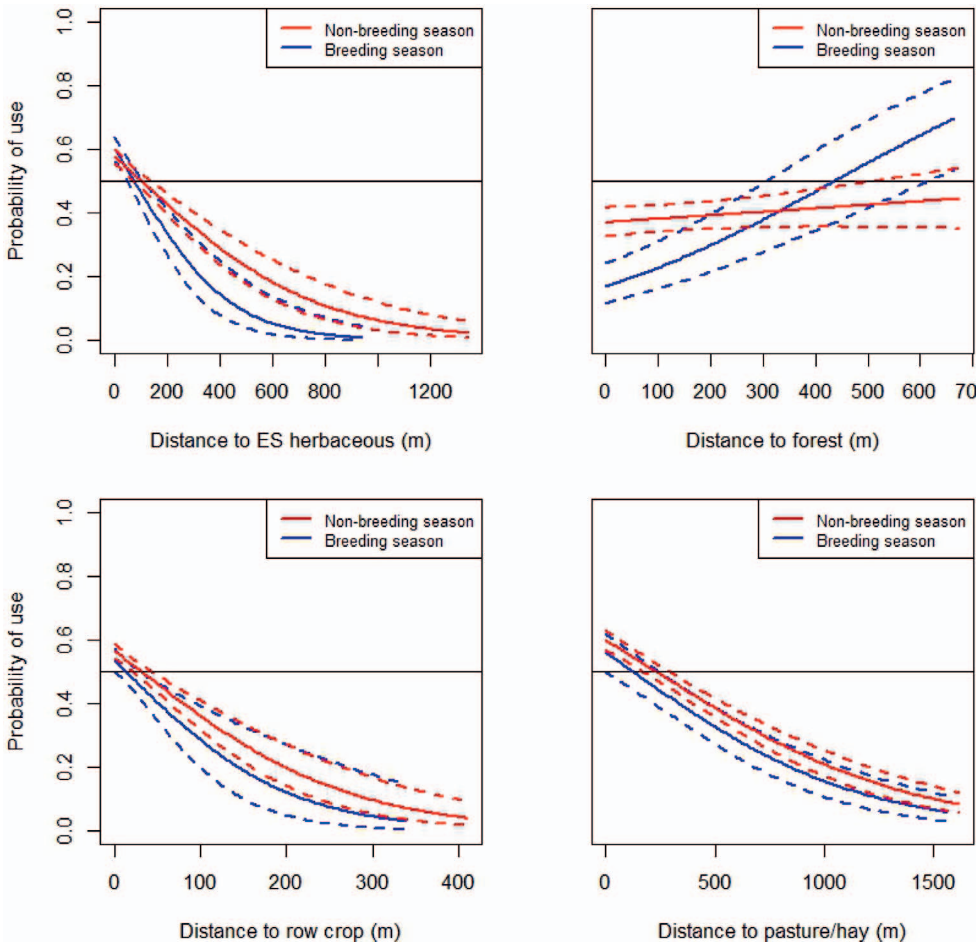

Fig. 5. Influence of distance to cover types on predicted probability of northern bobwhite use within the early successional woody cover type in southwestern Ohio (years and study sites combined). Dashed horizontal curves represent 95% confidence intervals. The horizontal line represents the 0.50 threshold of predicted probability of use.

areas during the non-breeding season and were more widely dispersed within cover types during the breeding season. This was especially evident on the Fee and Wildcat sites (Figures 9 and 12).

Column-wise differences in distances for used versus random points (Table 3) corresponded to the probability of use surfaces shown in Figures 9–12. Early successional herbaceous, ES woody, and pasture/hay cover types were closer than forest and row crop cover types to locations of radio-marked bobwhites within focal cover types than predicted from a random distribution of points. Probability surfaces predicted from distances to cover types revealed areas with high probabilities of use where radio-marked coveys and individual birds were located, but also other areas with high predicted probability of use that were not known to be occupied during the breeding and non-breeding seasons The Fee and Peach Orchard sites stood out from the Thurner and Wildcat sites in having large contiguous areas with low probabilities of use. Spatial distributions of radiolocations and areas with high probabilities of use differed between breeding and non-breeding seasons on all study sites with the possible exception of Peach Orchard. Areas with high probabilities of use were more fully occupied by radio-marked birds during the breeding season compared to distributions of radio-marked coveys during the non-breeding season on the Fee and Thurner sites (Figures 9 and 11).

DISCUSSION

Swift and Hannon (2010) suggested a critical threshold of 10-30% usable habitat for birds and mammals, below which fragmentation begins to negatively impact populations in addition to net habitat loss. Two methods that we used to estimate usable space provided very different results, each with their own implications for conservation of bobwhites. Sensitive mostly to relative use and abundance of cover types, the habitat selection ratio method produced estimated proportions of usable space that were lower (0.06-0.30) than distance to cover type estimates (0.30-0.53) which were sensitive to size, interspersion, and juxtaposition of cover types; and to the mobility of bobwhites that used those cover types. The difference in estimates from these two methods may be arbitrary; we selected a naïve cutoff (0.5 probability of use) to estimate usable space with the distance-based method.

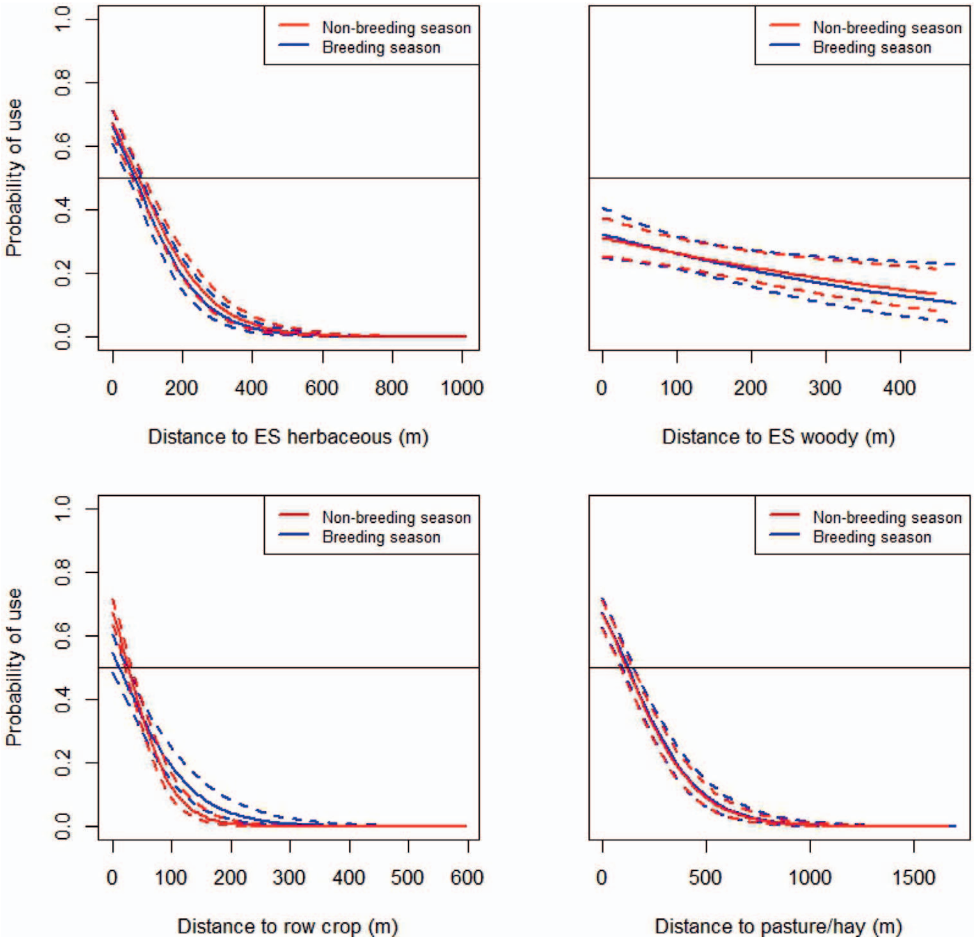

Fig. 6. Influence of distance to cover types on predicted probability of northern bobwhite use within the forest cover type in southwestern Ohio (years and study sites combined). Dashed horizontal curves represent 95% confidence intervals. The horizontal line represents the 0.50 threshold of predicted probability of use.

Estimates of usable space based on cover type selection ratios provided insights into temporal changes, while distance to cover type analyses based on distance to cover type provided insights into spatial variation in usable space within and among cover types. Though methods of analysis and interpretation of results differ between these approaches to estimating usable space, both can inform bobwhite habitat management and restoration. The habitat selection method quantifies usable space at a coarse scale that is more suited to regional conservation planning (Brennan 1991, and Williams et al. 2006) if habitat selection coefficients are generalized from studies conducted within a region. The distance-based method could be applied at regional scales but is better suited to targeting delivery of habitat conservation at the farm or management area scale. Generalized regional (i.e. by Bird Conservation Region) distance to cover type functions would need to be developed from empirical relationships such as we derived for our study areas.

The cover type selection ratio method revealed large seasonal variation in usable space. Low estimated proportions of usable space (<0.15) during the non-breeding season were associated with low use relative to high availability of row crops on our study sites. Proportions of usable space (selection ratio method) approached 0.35 on our study areas as bobwhites made greater use of row crop late in the breeding season. Row crop contributed the largest proportions of total areas of our study sites and was highly selected during brood-rearing (Liberati and Gates 2017, *in review*). Actively growing and mature row crops provide overhead concealment and bare ground during summer and early fall, allowing free movement and foraging by broods and coveys until fields are harvested (Janke and Gates 2013, Liberati 2011). Row crop fields are sources of food for bobwhites after fields are harvested (Hanson and Miller 1961, Guthery 1997). Although row crop fields averaged >100 ha of usable space (selection ratio method) across the four sites, row crop was still far more abundant on the landscape than necessary to meet the needs of bobwhites, as revealed by selection ratios that were <0.126 during the non-breeding season and <0.918 during the non-breeding season.

Seasonal comparisons of usable space based on cover type selection ratios assume that 1 ha of usable space during the non-breeding season equals 1 ha of usable space during the breeding season. This is a tenuous assumption because space use by bobwhites may differ

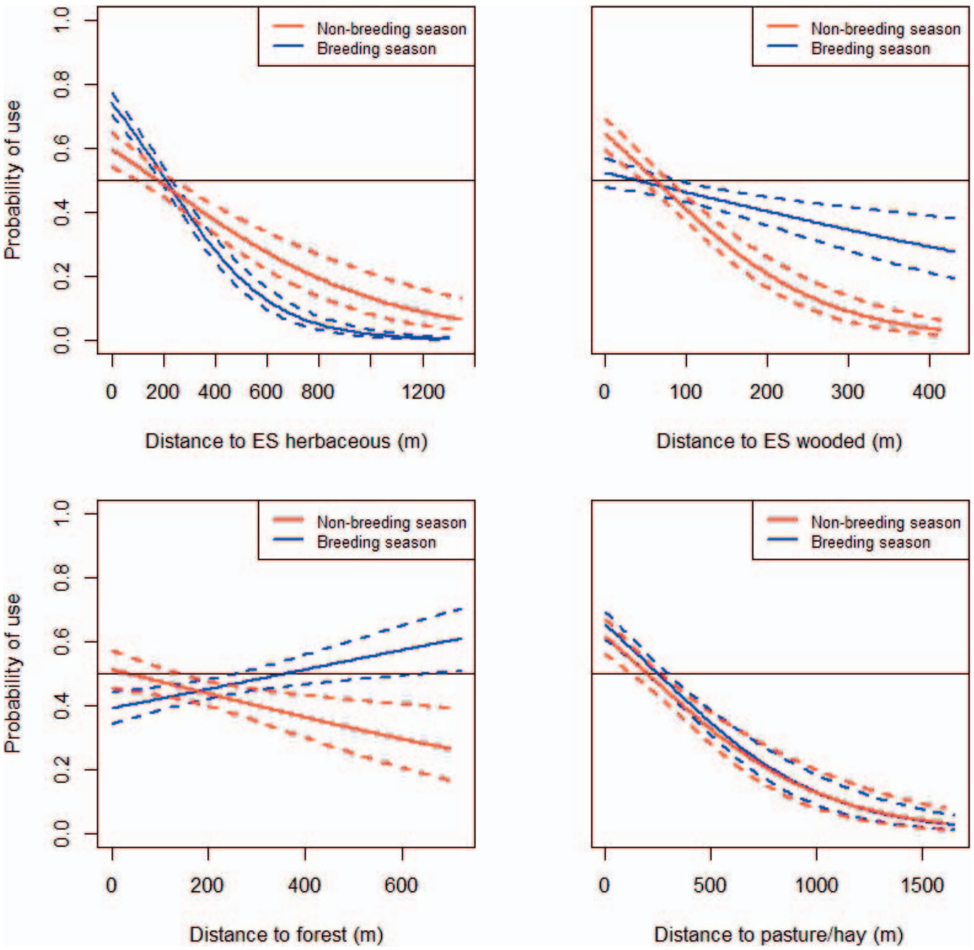

Fig. 7. Influence of distance to cover types on predicted probability of northern bobwhite use within the row crop cover type early in southwestern Ohio (years and study sites combined). Dashed horizontal curves represent 95% confidence intervals. The horizontal line represents the 0.50 threshold of predicted probability of use.

between breeding and non-breeding seasons. There was little or no overlap of covey home ranges during the non-breeding season in our study population (Janke et al. 2013). Home ranges of individual radio-marked birds overlapped during the breeding season (Liberati, unpublished data) when social units were single birds, mated pairs, or broods. Seasonal home range sizes also were larger for individual birds during the breeding season (mean = 125 ha; Liberati 2011) compared to coveys during the non-breeding season (mean = 26 ha; Janke and Gates 2013).

Our distance-based estimates of proportional usable space revealed overall differences between breeding and non-breeding seasons and only marginal differences (0.03-0.09) between seasons within cover types. Differences were more evident when we compared usable space among study sites. The Fee and Peach Orchard sites had the lowest crude densities of coveys (0.004-0.006 coveys/ha), and large contiguous areas of low use when probability of use was mapped as a response surface over cover type maps during the non-breeding season (mean probability = 0.30-0.31). The Thurner site had a somewhat higher mean crude density of coveys (0.007 coveys/ha) with a larger distance-based estimate of proportional usable space (0.43) during the non-breeding season. Crude densities of coveys were >2 times higher on the Wildcat site where mean probability of use was 0.45 during the non-breeding season.

Stoddard (1931: 374) stressed the importance of cover type diversity within a landscape and recommended a balance of open woodland, thickets, weedy and grassy fields, and cultivated ground to provide “the essentials in each [covey] range”. Distances between cover types are known to limit resource availability (Schroeder 1985, Guthery 1999), and dispersal (Williams et al. 2004). Cover types that Hanson and Miller (1961) deemed critical to supporting bobwhites (cultivated crop fields, herbaceous fields, and early successional shrubs and / forbs) were all represented in our distance to cover type models that predicted probability of use within cover types.

Cover types with the lowest mean selection ratios (e.g. forest, row crop, and pasture-hay) were also the cover types where radio-marked bobwhites were located closer to ES herbaceous and ES woody cover types than expected from random distributions of use points. We conclude that these cover types were not more fully utilized because field sizes on our study area were larger

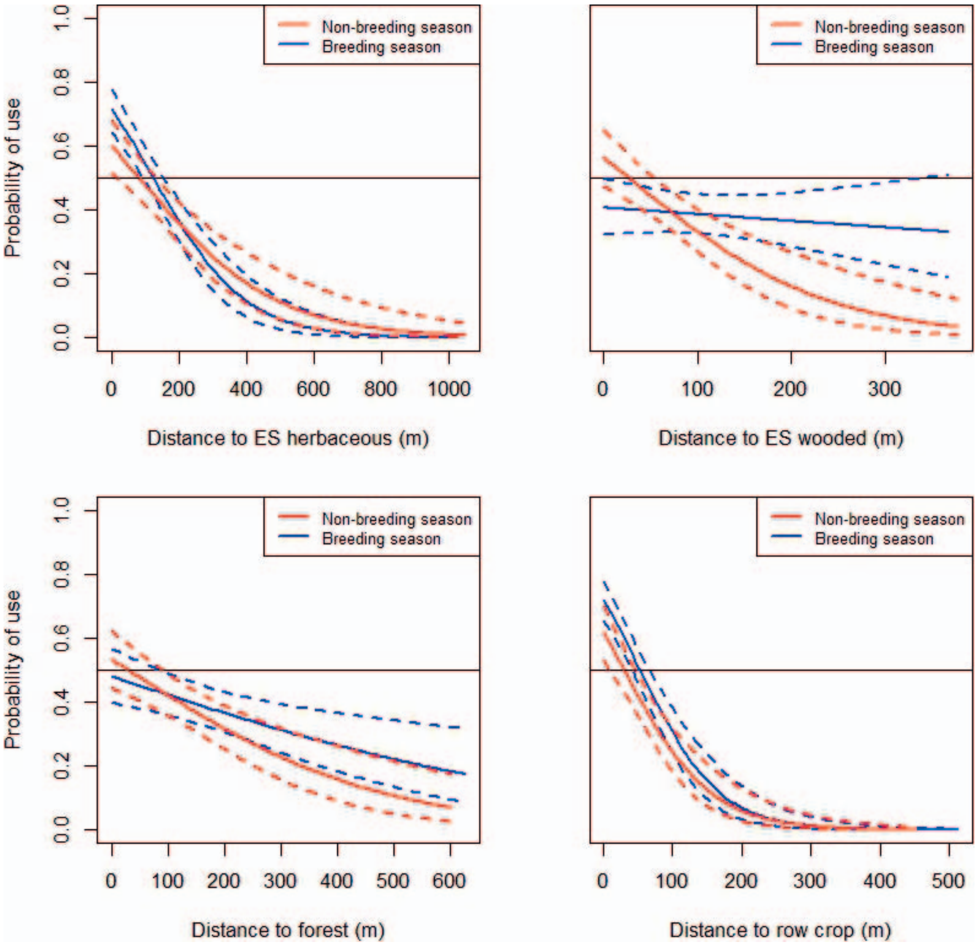

Fig. 8. Influence of distance to cover types on predicted probability of northern bobwhite use within the pasture/hay cover type in southwestern Ohio (years and study sites combined). Dashed horizontal curves represent 95% confidence intervals. The horizontal line represents the 0.50 threshold of predicted probability of use.

than necessary to supply food and cover requirements, or these habitats did not provide sufficient security when bobwhites moved farther into relatively open or homogeneous cover types, particularly during the non-breeding season. We found that bobwhites did not move far into cover types that lacked protective cover (forest, row crop and pasture/hay) during the non-breeding season and early stages of the breeding season. Used points averaged 73-135 m from nearest other cover types compared to random points that were located 118-222 m farther from nearest other cover types during breeding and non-breeding seasons. Affinity of bobwhites for habitat edges at least partially explains the low selection ratios we observed for forest, row crop, and pasture hay cover types that contributed to low overall estimates of usable space (selection ratio method), particularly during the non-breeding season.

Our results support Hanson and Miller's (1961) recommendation that establishing patches of ES woody cover 100-200 m apart in areas near ES herbaceous and row crop cover can improve usability. Proximity to ES woody cover strongly influenced probability of use within ES herbaceous and row crop cover types during the non-breeding season. Janke and Gates (2013) showed that selection of ES woody cover was highest during the non-breeding season but accounted for only 4% of total area of our study sites. The importance of ES woody cover is well established, particularly during the non-breeding season (Roseberry and Klimstra 1984, Schroeder 1985, Williams et al. 2000). Selection for ES woody and row crop cover types within the home range core indicated that bobwhites established home ranges where protective cover (e.g. woody edges) is close to food resources (e.g. row crops) during the non-breeding season (Janke and Gates (2013). Furthermore, row crop fields were used mostly within 10-53 m of ES woody and within 100-135 m of ES herbaceous cover types during breeding and non-breeding seasons.

With low selection ratios, forest and pasture/hay cover types contributed little or no usable space compared to other cover types. Usability was near zero for pasture/hay during most of the non-breeding season and increased only slightly during the breeding season. Pastures on our study sites were typically intensively grazed or mowed and rarely provided protective cover. Forest cover maintained a relatively low level of usability throughout each year with little or no seasonal variation, although bobwhites used interior areas of lightly grazed woodlots

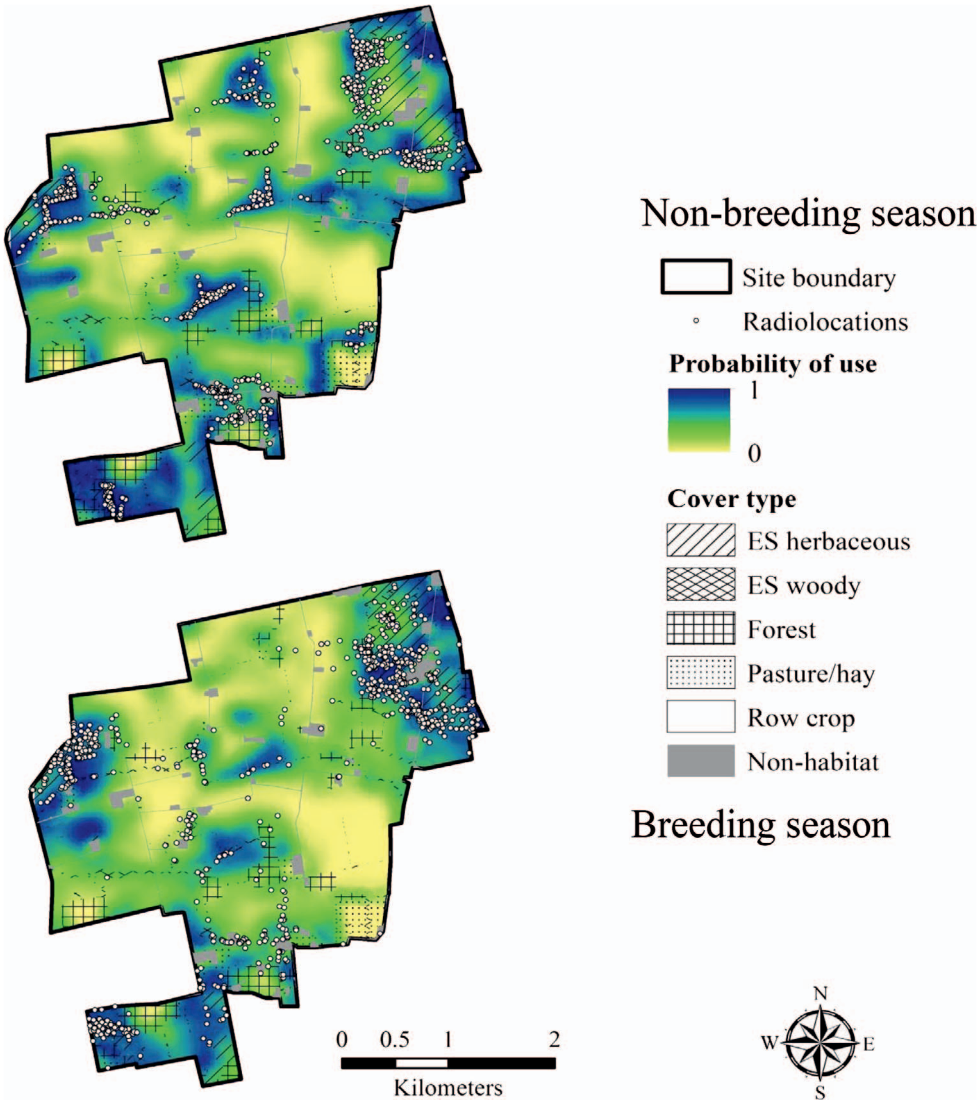

Fig. 9. Cover map and probability surface predicting use by northern bobwhites within the Fee study site in southwestern Ohio during 2009-2011 (years combined). Predicted use was based on distances between radio-locations of coveys and individuals and nearby cover types, pooled across sites, during the non-breeding and breeding seasons.

during the non-breeding season. Otherwise, individual birds or coveys used only very narrow forest edges near early successional herbaceous (50-66 m) and row crop (28-40 m) cover types during breeding and non-breeding seasons.

Our findings explain why others (Roseberry and Sudkamp 1998, Veech 2006, Bowling et al. 2014) found that bobwhite populations fare better in landscapes with more grassland, cropland, and woody edge than landscapes dominated by forest, pasture, or urban land cover. Schroeder (1985) suggested that bobwhite densities are maximized when food, cover, and nesting habitat occur in proper amounts and with proper spacing. Guthery (1999) suggested that there is no ideal configuration of different cover types (i.e. dispersion and quantity) and called this apparent plasticity "slack". Slack arises because bobwhites respond to general structural characteristics of vegetation and cover types that serve interchangeable purposes (Errington and Hamerstrom 1936). If bobwhites are attracted to ES woody cover for concealment and protection, it is reasonable to suggest that other cover types, such as ES herbaceous or forest cover, could serve as surrogates if vegetation structure is suitable for bobwhites (Guthery 1999).

Although slack exists in the ideal amount of various cover types within a management area, thresholds likely exist where too much or too little of any cover type reduces usability of an area (Guthery 1999). Cover patch size is known to affect bobwhite habitat suitability (Schroeder 1985). However, patch size was not included as a predictor variable in models that we used to develop probability of use maps for our study sites. We digitized all cover type patches and some may have been too small to benefit bobwhites.

Distance to ES herbaceous cover influenced year-round use of all cover types, though at greater distances than ES woody cover. As expected, comparing seasonal effects of distance to ES herbaceous cover suggested that

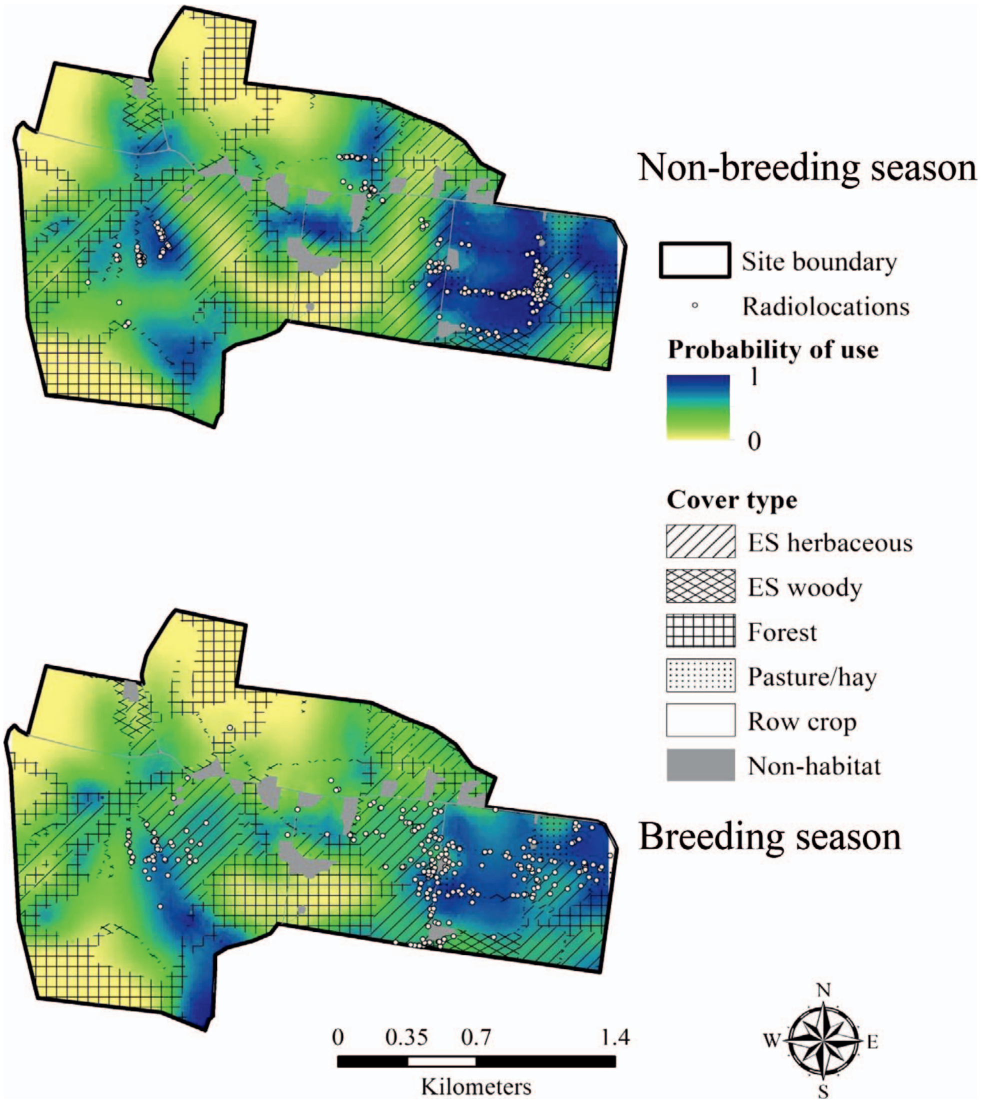

Fig. 10. Cover map and probability surface predicting use by northern bobwhite within the Peach Orchard study site in southwestern Ohio during 2009-2011 (years combined). Probability of use was based on distances between radio-locations of coveys and individuals and nearby cover types, pooled across sites, during the non-breeding and breeding seasons.

this cover type was more important during the breeding season compared to the non-breeding season. Early successional herbaceous fields provided cover, forage, and nesting habitat on our study sites during breeding (Liberati and Gates 2017, *in review*), and were the second most highly-selected cover type during non-breeding (Janke and Gates 2013).

We expected to observe a positive relationship between covey densities and usable space across study sites during the non-breeding season. The wildcat study site had the highest crude and ecological densities of coveys and the third lowest proportion of usable space (0.078) based on the habitat selection method. Crude and ecological covey densities were lower on the Fee, Peach, and Thurner sites where the proportions of usable space (habitat selection method) ranged from 0.073 to 0.188. The Wildcat site averaged higher probabilities of use (distance-based method) followed in similar rank order as crude or ecological densities by the Thurner, Peach Orchard, and Fee sites. The cover type selection-based estimate of usable space could only be used to compare study sites and did not represent fine-scale variation within sites like the distance-based method which provided spatially explicit and finer-scale estimates of usable space on a continuous 0 to 1 scale.

Absence or low density of a species does not necessarily mean that habitat conditions are unsuitable (Wiens 1989). Population density and demography also determine occupancy (Wiens et al. 1987, Haila et al. 1996). Demographic sensitivity analyses of empirically-determined vital rates revealed that reproductive rates were insufficient to offset mortality during the non-breeding season (Gates et al.2012). As a result, we expected to find that some usable space was unoccupied when radio-locations of individual birds and coveys were overlaid on use probability maps. Consistent with higher ecological densities of coveys, usable areas were more fully occupied by radio-marked birds during the non-

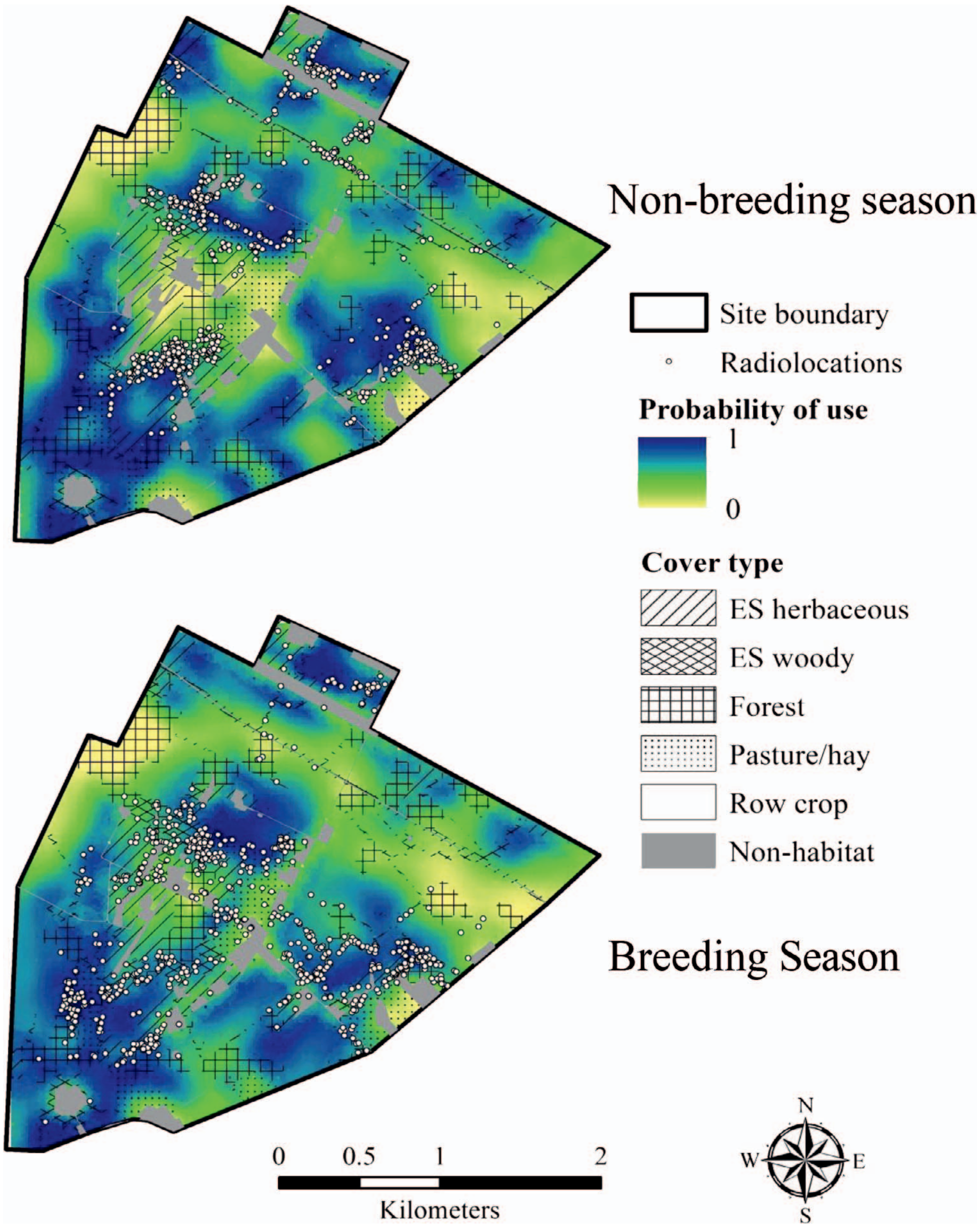

Fig. 11. Cover map and probability surface predicting use by northern bobwhite within the Thurner study site in southwestern Ohio during 2009-2011 (years combined). Probability of use was based on distances between radio-locations of coveys and individuals and nearby cover types, pooled across sites, during the non-breeding and breeding seasons.

breeding season on the Wildcat site, while usable areas of Thurner, Fee, and Peach were only partially occupied by radio-marked birds when we overlaid radio-locations on predicted probability of use maps. Underutilization of usable space could also be explained by differences in vegetation structure and composition at the microhabitat scale. Wiley (2012) showed that use of cover types was affected by ground cover, overhead cover, and visual obstruction. Macro-habitat variables not included in our analyses of usable space (e.g. patch size and configuration) may have affected space use by bobwhites (Kopp et al. 1998).

Availability of suitable habitat is thought to be the most limiting environmental factor in northern areas of bobwhite range (Guthery 1997). Survival was negatively associated with depth and duration of snow cover during December-February in our study population (Janke and Gates 2012, Knapik 2015). Furthermore, individual survival during periods of prolonged snow cover increased with ES woody edge density within 95 m of areas used by radio-marked bobwhites (Janke et al. 2015). We found that bobwhites used points within focal cover types that were 44-92 m closer to the ES woody cover type than expected from random use during the non-breeding season. We contend that growth of our study population is limited by availability of protective cover (e.g. ES woody) near food sources (e.g. row crop), exposing bobwhites to high levels of predation during

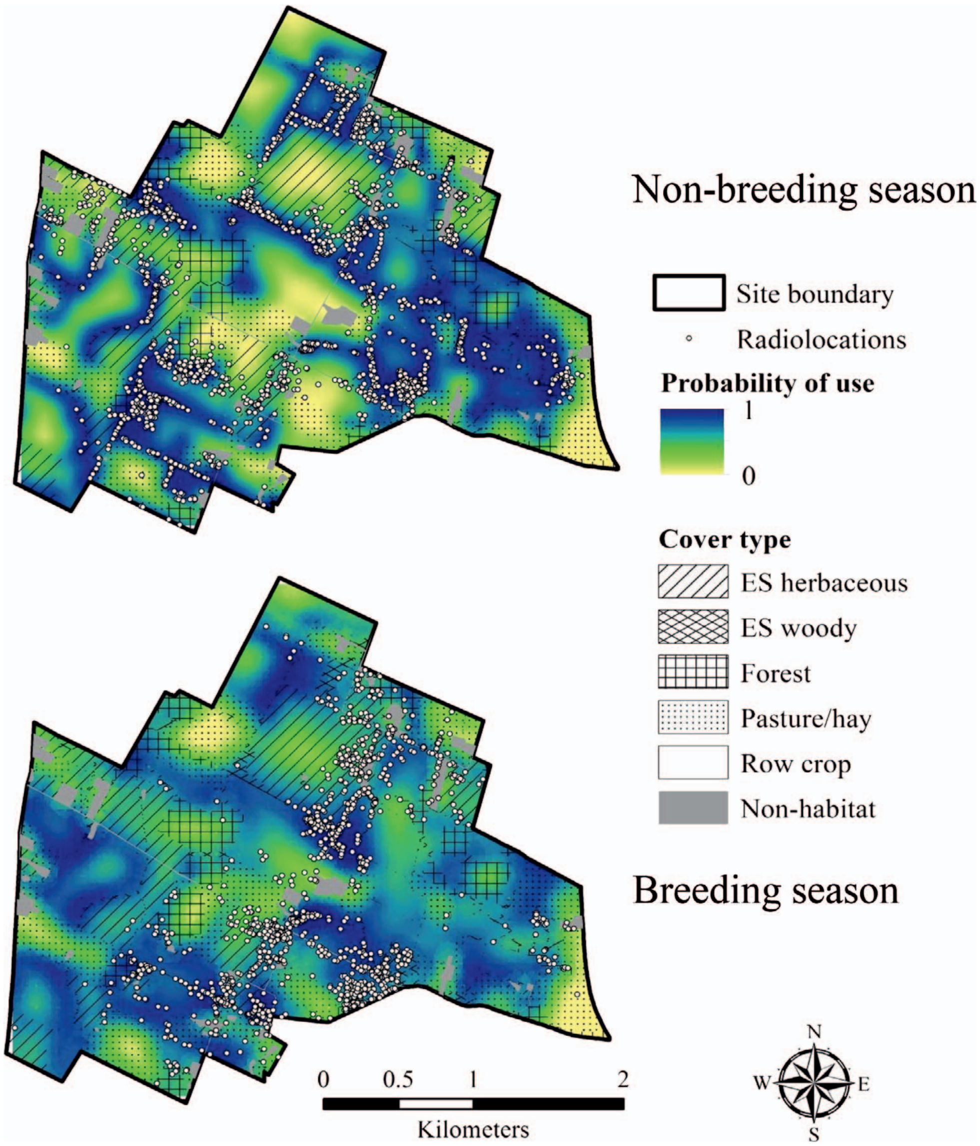

Fig. 12. Cover map and probability surface predicting use by northern bobwhite within the Wildcat study site in southwestern Ohio during 2009-2011 (years combined). Probability of use was based on distances between radio-locations of coveys and individuals and nearby cover types, pooled across sites, during the non-breeding and breeding season.

winters with prolonged snow cover that covers food resources. Roseberry and Sudkamp (1998) emphasized the importance of woody edge as a habitat component that sustained bobwhite populations in Illinois. Evans et al. (2013) found only small increases in bobwhite covey densities associated with establishment of herbaceous field borders in the Eastern Tallgrass Prairie region that included our study areas. All of this points to woody cover and not herbaceous cover as the most limiting habitat factor in southwestern Ohio.

Habitat conservation for grassland- or early succession-dependent wildlife has focused on converting crop fields to perennial herbaceous cover. This strategy follows recommendations that range-wide recovery of northern bobwhite populations should focus on increasing usable space at the regional level by restoring native grasses and forbs with the assumption that populations are limited by reproduction (Burger et al. 2006). This may be true in southern areas of bobwhite range but we have argued that bobwhite populations on our study areas (and possibly in other northern areas of bobwhite range) are most limited by protective cover near food sources during the non-breeding season (Gates et al. 2012). This is not to say that sustaining reproduction by providing adequate nesting and brood-rearing habitat is not essential to conserving bobwhite populations throughout their range.

Small proportional changes in primary land use can leverage disproportionate increases in grassland and edge-dependent birds during winter (Evans et al. 2013). The strong association of bobwhites with habitat edges such as we and many others before us have demonstrated suggests that buffer strips of early successional woody vegetation or native grasses and forbs can be added to agricultural landscapes to sustain bobwhite populations. Establishing buffers has produced positive but mixed results that vary regionally Evans et al. 2013) with, amount of forest land (Riddle et al. 2008), predator reduction (Palmer et al. 2005) and regional abundance of bobwhites (Bowling et al. 2014).

MANAGEMENT IMPLICATIONS

Conservation challenges are intensified in working landscapes where production-focused land uses create inhospitable conditions for bobwhites. Conserving early successional woody and herbaceous cover types are essential to sustaining bobwhite populations in Midwestern agricultural landscapes. This is challenging because habitat acquisition, protection, and maintenance are costly, especially when agricultural commodity prices rise. Removing land from agricultural production also limits earning potential of private-owned working lands, thereby diminishing incentives for landowners to conserve wildlife habitat. Private lands managers must work within the constraints of technological, policy, and economic forces that are beyond their control, and seek ways to integrate bobwhite conservation with production agriculture.

Though certainly beneficial, converting large contiguous tracts of cropland to perennial cover may not be the most efficient way to improve habitat for bobwhites on agricultural working lands where opportunities are limited or cost-prohibitive. We found that use of preferred cover types by bobwhites was influenced by distance to other cover types. A more practical alternative might be to create and sustain early successional cover along wooded edges (including woodlots) near cover types that provide critical food and cover (e.g. ES herbaceous and row crop) throughout the annual life cycle. Adding small tracts or buffer strips of ES woody and herbaceous cover near habitats that are less selected for by bobwhites (e.g. row crop and pasture/hay) could leverage increased usable space while minimizing impact on production agriculture. Most radio-marked bobwhites were located in focal cover types within 50-250 m of other cover types so conserving small (0.25-6.25 ha) areas of ES herbaceous and woody cover in areas that are difficult to farm should increase usable space if they are strategically placed relative to other cover types that provide food and protective cover during breeding and non-breeding seasons.

Locations of radio-marked bobwhites were more strongly associated with edges during the non-breeding season than during the breeding season. Our study sites were characterized by "hard edges" of maturing woodlots adjacent to open cropland. More attention should be given to enhancing protective cover along woodlot edges that adjoin row cropland to improve non-breeding habitat. Adding buffers of ES herbaceous habitat near woody edges could provide nesting and brood-rearing habitat near protective cover. Reduction of tree basal area to promote growth of early successional vegetation (i.e. "edge feathering") was implemented during 2012 and 2013 to improve protective cover on the Fee and Peach Orchard sites (Brooks 2015, Knapik 2015). With distance to cover type functions similar to what we used, a digital habitat coverage and GIS, managers can identify gaps where focal habitat restoration and management are best applied to leverage increases in usable space while minimizing impact on the capacity of working lands to produce agricultural or forest products.

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Appendix 1. Cover type selection and usable space for 51 individual northern bobwhites on four study sites (combined) in southwestern Ohio during the breeding season in 2010.

Month	Cover type	No. radio-locations	Prop. use (p_i)	Prop. available (a_i)	Selection ratio (p_i/a_i)	Prop. Usable (u_i)	Usable space (U_i in ha)	Total area (A_i in ha)
April	Row Crop	99	0.162	0.579	0.280	0.040	62.8	1555.5
	Pasture Hay	36	0.059	0.080	0.740	0.107	22.8	213.8
	Forest	102	0.167	0.123	1.360	0.196	64.7	329.8
	ES Woody	172	0.282	0.041	6.934	1.000	109.1	109.1
	ES Herb	193	0.316	0.130	2.434	0.351	122.4	348.6
	Non Habitat	9	0.015	0.048	0.305	0.044	5.7	129.7
May	Row Crop	73	0.157	0.579	0.271	0.064	99.5	1555.5
	Pasture Hay	31	0.067	0.080	0.838	0.198	42.3	213.8
	Forest	62	0.133	0.123	1.086	0.256	84.5	329.8
	ES Woody	80	0.172	0.041	4.238	1.000	109.1	109.1
	ES Herb	200	0.430	0.130	3.314	0.782	272.6	348.6
	Non Habitat	19	0.041	0.048	0.846	0.200	25.9	129.7
June	Row Crop	104	0.271	0.579	0.468	0.110	171.8	1555.5
	Pasture Hay	6	0.016	0.080	0.196	0.046	9.9	213.8
	Forest	11	0.029	0.123	0.233	0.055	18.2	329.8
	ES Woody	39	0.102	0.041	2.502	0.591	64.4	109.1
	ES Herb	211	0.549	0.130	4.234	1.000	348.6	348.6
	Non Habitat	13	0.034	0.048	0.701	0.166	21.5	129.7
July	Row Crop	76	0.394	0.579	0.680	0.247	384.0	1555.5
	Pasture Hay	5	0.026	0.080	0.326	0.118	25.3	213.8
	Forest	7	0.036	0.123	0.295	0.107	35.4	329.8
	ES Woody	21	0.109	0.041	2.680	0.973	106.1	109.1
	ES Herb	69	0.358	0.130	2.755	1.000	348.6	348.6
	Non Habitat	15	0.078	0.048	1.610	0.584	75.8	129.7
August	Row Crop	52	0.437	0.579	0.755	0.271	421.6	1555.5
	Pasture Hay	11	0.092	0.080	1.162	0.417	89.2	213.8
	Forest	7	0.059	0.123	0.479	0.172	56.8	329.8
	ES Woody	5	0.042	0.041	1.035	0.372	40.5	109.1
	ES Herb	43	0.361	0.130	2.784	1.000	348.6	348.6
	Non Habitat	1	0.008	0.048	0.174	0.063	8.1	129.7
September	Row Crop	34	0.531	0.579	0.918	0.265	412.0	1555.5
	Pasture Hay	5	0.078	0.080	0.982	0.283	60.6	213.8
	Forest	12	0.188	0.123	1.527	0.441	145.4	329.8
	ES Woody	9	0.141	0.041	3.464	1.000	109.1	109.1
	ES Herb	3	0.047	0.130	0.361	0.104	36.4	348.6
	Non Habitat	1	0.016	0.048	0.324	0.093	12.1	129.7

Appendix 2. Cover type selection and usable space for 47 individual northern bobwhites on four study sites (combined) in southwestern Ohio during the breeding season in 2011.

Month	Cover type	No. radio-locations	Prop. use (p_i)	Prop. available (a_i)	Selection ratio (p_i/a_i)	Prop. Usable (u_i)	Usable space (U_i in ha)	Total area (A_i in ha)
April	Row Crop	21	0.030	0.553	0.055	0.007	12.4	1802.1
	Pasture Hay	35	0.050	0.090	0.557	0.070	20.7	294.1
	Forest	217	0.312	0.131	2.381	0.301	128.3	426.8
	ES Woody	240	0.345	0.044	7.921	1.000	141.9	141.9
	ES Herb	178	0.256	0.134	1.902	0.240	105.2	438.1
	Non Habitat	5	0.007	0.048	0.150	0.019	3.0	156.1
May	Row Crop	66	0.122	0.553	0.221	0.029	51.7	1802.1
	Pasture Hay	38	0.070	0.090	0.778	0.101	29.8	294.1
	Forest	96	0.177	0.131	1.355	0.176	75.3	426.8
	ES Woody	181	0.335	0.044	7.685	1.000	141.9	141.9
	ES Herb	151	0.279	0.134	2.076	0.270	118.4	438.1
	Non Habitat	9	0.017	0.048	0.347	0.045	7.1	156.1
June	Row Crop	23	0.067	0.553	0.122	0.013	23.6	1802.1
	Pasture Hay	33	0.096	0.090	1.069	0.115	33.9	294.1
	Forest	39	0.114	0.131	0.871	0.094	40.1	426.8
	ES Woody	138	0.404	0.044	9.269	1.000	141.9	141.9
	ES Herb	102	0.298	0.134	2.219	0.239	104.9	438.1
	Non Habitat	7	0.020	0.048	0.427	0.046	7.2	156.1
July	Row Crop	62	0.191	0.553	0.346	0.083	149.1	1802.1
	Pasture Hay	13	0.040	0.090	0.445	0.106	31.3	294.1
	Forest	48	0.148	0.131	1.131	0.270	115.4	426.8
	ES Woody	59	0.182	0.044	4.183	1.000	141.9	141.9
	ES Herb	127	0.392	0.134	2.916	0.697	305.4	438.1
	Non Habitat	15	0.046	0.048	0.966	0.231	36.1	156.1
August	Row Crop	75	0.419	0.553	0.758	0.268	483.7	1802.1
	Pasture Hay	4	0.022	0.090	0.248	0.088	25.8	294.1
	Forest	17	0.095	0.131	0.725	0.257	109.6	426.8
	ES Woody	22	0.123	0.044	2.823	1.000	141.9	141.9
	ES Herb	60	0.335	0.134	2.494	0.883	386.9	438.1
	Non Habitat	1	0.006	0.048	0.117	0.041	6.4	156.1
September	Row Crop	9	0.409	0.553	0.740	0.177	319.2	1802.1
	Pasture Hay	2	0.091	0.090	1.007	0.241	70.9	294.1
	Forest	1	0.045	0.131	0.347	0.083	35.5	426.8
	ES Woody	4	0.182	0.044	4.177	1.000	141.9	141.9
	ES Herb	6	0.273	0.134	2.029	0.486	212.8	438.1
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	156.1

Appendix 3. Cover type selection and usable space for 26 northern bobwhites coveys on four study sites (combined) in southwestern Ohio during the non-breeding season in 2009-2010.

Month	Cover type	No. radio-locations	Prop. use (p_i)	Prop. available (a_i)	Selection ratio (p_i / a_i)	Prop. Usable (u_i)	Usable space (U_i in ha)	Total area (A_i in ha)
October	Row Crop	0	0.000	0.579	0.000	0.000	0.0	1555.5
	Pasture Hay	2	0.050	0.080	0.628	0.038	8.1	213.8
	Forest	3	0.075	0.123	0.611	0.037	12.1	329.8
	ES Woody	27	0.675	0.041	16.627	1.000	109.1	109.1
	ES Herb	8	0.200	0.130	1.541	0.093	32.3	348.6
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	129.7
November	Row Crop	12	0.051	0.579	0.087	0.010	16.0	1555.5
	Pasture Hay	13	0.055	0.080	0.689	0.081	17.3	213.8
	Forest	35	0.148	0.123	1.203	0.141	46.5	329.8
	ES Woody	82	0.346	0.041	8.523	1.000	109.1	109.1
	ES Herb	95	0.401	0.130	3.089	0.362	126.3	348.6
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	129.7
December	Row Crop	12	0.035	0.579	0.060	0.005	8.2	1555.5
	Pasture Hay	18	0.052	0.080	0.658	0.058	12.3	213.8
	Forest	59	0.172	0.123	1.397	0.123	40.5	329.8
	ES Woody	159	0.462	0.041	11.386	1.000	109.1	109.1
	ES Herb	95	0.276	0.130	2.128	0.187	65.2	348.6
	Non Habitat	1	0.003	0.048	0.060	0.005	0.7	129.7
January	Row Crop	40	0.074	0.579	0.128	0.011	17.6	1555.5
	Pasture Hay	9	0.017	0.080	0.210	0.019	4.0	213.8
	Forest	82	0.152	0.123	1.241	0.109	36.1	329.8
	ES Woody	248	0.461	0.041	11.355	1.000	109.1	109.1
	ES Herb	159	0.296	0.130	2.277	0.201	69.9	348.6
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	129.7
February	Row Crop	21	0.053	0.579	0.091	0.006	9.3	1555.5
	Pasture Hay	2	0.005	0.080	0.063	0.004	0.9	213.8
	Forest	63	0.158	0.123	1.283	0.085	27.9	329.8
	ES Woody	246	0.615	0.041	15.149	1.000	109.1	109.1
	ES Herb	66	0.165	0.130	1.271	0.084	29.3	348.6
	Non Habitat	2	0.005	0.048	0.104	0.007	0.9	129.7
March	Row Crop	29	0.097	0.579	0.168	0.013	20.3	1555.5
	Pasture Hay	9	0.030	0.080	0.378	0.029	6.3	213.8
	Forest	73	0.244	0.123	1.989	0.155	51.0	329.8
	ES woody	156	0.522	0.041	12.852	1.000	109.1	109.1
	ES Herb	31	0.104	0.130	0.799	0.062	21.7	348.6
	Non Habitat	1	0.003	0.048	0.069	0.005	0.7	129.7

Appendix 4. Cover type selection and usable space for 32 northern bobwhites coveys on four study sites (combined) in southwestern Ohio during the non-breeding season in 2010-2011.

Month	Cover type	No. radio-locations	Prop. use (p_i)	Prop. available (a_i)	Selection ratio (p_i /a_i)	Prop. Usable (u_i)	Usable space (U_i in ha)	Total area (A_i in ha)
October	Row Crop	7	0.033	0.553	0.059	0.006	11.2	1802.1
	Pasture Hay	28	0.131	0.090	1.457	0.152	44.6	294.1
	Forest	38	0.178	0.131	1.362	0.142	60.6	426.8
	ES Woody	89	0.418	0.044	9.598	1.000	141.9	141.9
	ES Herb	51	0.239	0.134	1.781	0.186	81.3	438.1
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	156.1
November	Row Crop	9	0.028	0.553	0.050	0.006	10.6	1802.1
	Pasture Hay	27	0.083	0.090	0.924	0.108	31.7	294.1
	Forest	97	0.299	0.131	2.286	0.266	113.7	426.8
	ES Woody	121	0.373	0.044	8.579	1.000	141.9	141.9
	ES Herb	68	0.210	0.134	1.561	0.182	79.7	438.1
	Non Habitat	2	0.006	0.048	0.129	0.015	2.3	156.1
December	Row Crop	12	0.034	0.553	0.061	0.006	11.4	1802.1
	Pasture Hay	7	0.020	0.090	0.220	0.023	6.6	294.1
	Forest	126	0.357	0.131	2.725	0.279	119.2	426.8
	ES Woody	150	0.425	0.044	9.761	1.000	141.9	141.9
	ES Herb	57	0.161	0.134	1.201	0.123	53.9	438.1
	Non Habitat	1	0.003	0.048	0.059	0.006	0.9	156.1
January	Row Crop	29	0.053	0.553	0.096	0.008	15.1	1802.1
	Pasture Hay	7	0.013	0.090	0.141	0.012	3.6	294.1
	Forest	132	0.240	0.131	1.836	0.161	68.6	426.8
	ES Woody	273	0.497	0.044	11.423	1.000	141.9	141.9
	ES Herb	108	0.197	0.134	1.463	0.128	56.1	438.1
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	156.1
February	Row Crop	22	0.043	0.553	0.077	0.007	12.6	1802.1
	Pasture Hay	2	0.004	0.090	0.043	0.004	1.1	294.1
	Forest	126	0.244	0.131	1.861	0.170	72.4	426.8
	ES Woody	247	0.478	0.044	10.975	1.000	141.9	141.9
	ES Herb	115	0.222	0.134	1.655	0.151	66.1	438.1
	Non Habitat	5	0.010	0.048	0.202	0.018	2.9	156.1
March	Row Crop	19	0.033	0.553	0.060	0.005	9.0	1802.1
	Pasture Hay	7	0.012	0.090	0.135	0.011	3.3	294.1
	Forest	119	0.207	0.131	1.577	0.132	56.5	426.8
	ES Woody	299	0.519	0.044	11.924	1.000	141.9	141.9
	ES Herb	128	0.222	0.134	1.653	0.139	60.7	438.1
	Non Habitat	4	0.007	0.048	0.145	0.012	1.9	156.1

Appendix 5. Standardized logistic regression coefficients (β) with standard errors (SE) of models selected by stepwise selection to predict probability of use of 5 cover types as a function of distance to other cover types for northern bobwhites during the breeding season in southwestern Ohio. Years and study sites were combined for analyses.

Cover Type	Covariate	B	SE(β)	*P*
ES Herbaceous	Intercept	-0.1029	0.0412	0.0125
	ESW	0.0034	0.0491	0.9440
	F	0.2731	0.0400	<0.0001
	RC	-0.2518	0.0433	<0.0001
	PH	-0.0758	0.0444	0.0876
	ESW*PH	0.3084	0.0418	<0.0001
	F*RC	-0.2263	0.0438	<0.0001
	F*PH	0.1140	0.0434	0.0086
ES Wooded	Intercept	-0.3394	0.1161	0.0035
	ESH	-0.9916	0.1703	<0.0001
	F	0.6669	0.0695	<0.0001
	RC	-0.7381	0.1826	<0.0001
	PH	-0.5782	0.0733	<0.0001
	ESH*RC	-0.8833	0.2709	0.0011
	ESH*PH	-0.2543	0.1006	0.0114
	F*RC	-0.2089	0.0769	0.0066
	F*PH	0.2752	0.0789	0.0005
	RC*PH	0.1411	0.0771	0.0671
Forest	Intercept	-1.0450	0.1366	<0.0001
	ESH	-1.8211	0.1665	<0.0001
	ESW	-0.2333	0.0957	0.0148
	RC	-1.2949	0.1608	<0.0001
	PH	-1.9038	0.1854	<0.0001
	ESH*ESW	0.1660	0.1073	0.1217
	ESH*RC	-0.7011	0.1540	<0.0001
	ESH*PH	-1.4646	0.1932	<0.0001
	ESW*PH	0.5535	0.1294	<0.0001
	RC*PH	-1.3344	0.1979	<0.0001
Row Crop	Intercept	-0.1549	0.0621	0.0126
	ESH	-1.1520	0.0816	<0.0001
	ESW	-0.2197	0.0636	0.0006
	F	0.1934	0.0627	0.0020
	PH	-0.6681	0.0719	<0.0001
	ESH*PH	-0.4344	0.0991	<0.0001
	ESH*F	0.1155	0.0723	0.1100
	ESW*F	-0.5399	0.0765	<0.0001
Pasture/Hay	Intercept	-0.4558	0.1331	0.0006
	ESH	-1.3371	0.1931	<0.0001
	ESW	-0.0683	0.1027	0.5058
	F	-0.3283	0.1096	0.0027
	RC	-1.3747	0.1865	<0.0001
	ESH*RC	-0.9253	0.2429	0.0001
	ESW*RC	0.1852	0.0883	0.0361
	F*RC	-0.2533	0.1517	0.0949

[a] Cover type to which models were applied

[b] RC = row crop; PH = pasture/hay; F = forest; ESW = early successional woody; ESH = early successional herbaceous

Appendix 6. Standardized logistic regression coefficients (β) standard errors (SE) of models selected by stepwise selection to predict probability of use of 5 cover types as a function of distance to other cover types for northern bobwhites during the non-breeding season in southwestern Ohio. Years and study sites were combined for analyses.

Cover Type	Covariate	B	SE(β)	*P*
ES Herbaceous	Intercept	-0.1373	0.0490	0.0051
	ESW	-0.5248	0.0616	<0.0001
	F	0.0411	0.0481	0.3934
	RC	-0.9449	0.0614	<0.0001
	PH	0.0619	0.0461	0.1798
	ESW*PH	0.1640	0.0472	0.0005
	F*PH	0.1455	0.0546	0.0077
	RC*PH	0.1133	0.0568	0.0460
ES Wooded	Intercept	-0.1020	0.0521	0.0501
	ESH	-0.5785	0.0733	<0.0001
	F	0.1246	0.0407	0.0022
	RC	-0.5864	0.0788	<0.0001
	PH	-0.5001	0.0431	<0.0001
	ESH*F	-0.2710	0.0492	<0.0001
	ESH*RC	-0.2642	0.1212	0.0293
	ESH*PH	-0.1257	0.0548	0.0219
	F*PH	0.1277	0.0455	0.0050
Forest	Intercept	-1.0560	0.1203	<0.0001
	ESH	-1.8874	0.1537	<0.0001
	ESW	-0.2108	0.0669	0.0016
	RC	-1.9753	0.1624	<0.0001
	PH	-1.7884	0.1420	<0.0001
	ESH*RC	-1.4054	0.1779	<0.0001
	ESH*PH	-0.9724	0.1303	<0.0001
	RC*PH	-1.1198	0.1642	<0.0001
Row Crop	Intercept	-0.2385	0.0792	0.0026
	ESH	-0.5956	0.0912	<0.0001
	ESW	-0.8432	0.0885	<0.0001
	F	-0.2249	0.0798	0.0048
	PH	-0.6358	0.0922	<0.0001
	ESH*ESW	0.2415	0.0921	0.0088
	ESH*PH	-0.7202	0.1242	<0.0001
	ESW*F	-0.3475	0.0971	0.0003
	ESW*PH	0.1289	0.0884	0.1449
	F*PH	0.2008	0.0861	0.0197
Pasture/Hay	Intercept	-0.5694	0.1407	0.0001
	ESH	-0.8671	0.1689	<0.0001
	ESW	-0.8150	0.1845	<0.0001
	F	-1.1518	0.1887	<0.0001
	RC	-0.6104	0.1415	<0.0001
	ESH*ESW	-0.7557	0.2279	0.0009
	ESH*RC	-0.3883	0.2431	0.1102
	ESW*F	-1.1152	0.1886	<0.0001
	RC*F	0.3547	0.1955	0.0696

[a] Cover type to which models were applied

[b] RC = row crop; PH = pasture/hay; F = forest; ESW = early successional woody; ESH = early successional herbaceous

TEMPERATURE ASSESSMENT ON A RECLAIMED SURFACE MINE DURING NORTHERN BOBWHITE BREEDING SEASON: CONSIDERATIONS FOR HABITAT MANAGEMENT

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ABSTRACT

Ground-level air temperatures were assessed within 4 distinct habitat areas on a managed reclaimed surface mine at Peabody Wildlife Management Area, Kentucky, 26 June–17 July 2015, during the northern bobwhite (*Colinus virginianus*) brood season. Habitat consisted of disked and nondisked areas of native grass and an invasive species, sericea lespedeza (*Lespedeza cuneata*). Disked areas offered more open space for bobwhite mobility and experienced higher average temperatures than nondisked sites. Although statistically significant, differences in air temperature between disked and nondisked areas were likely too small to have practical implications for bobwhite habitat management in Kentucky under current climatic conditions. This will likely change in the future as the regional climate warms and periods of excessive heat are more likely to occur. Consequently, managers may want to consider microclimate when making management decisions.

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Key words: *Colinus virginianus,* conservation, habitat management, *Lespedeza cuneata,* northern bobwhite, Peabody WMA, reclaimed surface mine, temperature

More than 8 billion tons of coal have been extracted from Kentucky's Eastern and Western Coalfields since the state's first commercial coal mine opened in 1820 (KGS 2016). Following the removal of the coal deposits, thousands of hectares of mine lands have undergone reclamation and wildlife managers are tasked to find the best way(s) to transform the postreclamation landscape into productive habitat. Several researchers have studied the viability of reclaimed mine land as habitat for grassland birds (e.g., Scott et al. 2002, Monroe and Ritchison 2005, Galligan et al. 2006). Although regulations encourage mining companies to establish native vegetation during the reclamation process, nonnative species are often planted instead, particularly sericea lespedeza (*Lespedeza cuneata*). Sericea provides little value to northern bobwhite (*Colinus virginianus*) as habitat because it tends to grow very densely, its seeds are indigestible by bobwhite, and it may limit the abundance of insects that bobwhite eat (Blocksome 2006). Sericea presents challenges for northern bobwhite conservation as it spreads readily and produces large numbers of seeds that can remain viable for many years and grows in virtually any soil type. Controlling sericea requires regular treatment over a number of years and

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there is no known method for its eradication (Silliman and Maccarone 2005).

Prior research on a reclaimed surface mine in western Kentucky has shown that bobwhite populations exhibit low production of young, lower than normal hatchability of eggs, and extremely low adult survival in the summer (Brooke 2015, Brooke et al. 2015, Peters et al. 2015). In a 4-year study, Peters et al. (2015) found that bobwhite survival varied annually, ranging from 0.139 (SE = 0.031) to 0.301 (SE = 0.032), and seasonally (summer, 0.148 [SE = 0.015]; winter, 0.281 [SE = 0.022]). Excessive heat may contribute to lower summer survival and production in this area because high temperatures are known to negatively impact bobwhites. High summer temperatures can limit bobwhite reproduction (Guthery et al. 1988), and hyperthermia reduces avian embryo survival (Webb 1987). Reyna and Burggren (2012) specifically identified 40° C as the upper limit for bobwhite egg survival and Guthery et al. (2005) identified 39° C as a threshold where quail become hyperthermic. Guthery et al. (2005) also found that approximately 90% of incubating adult bobwhites tracked in their study were employing gular flutter to regulate body temperature when air temperature exceeded 35° C. This thermoregulatory behavior may interact with food and water availability because gular flutter dramatically increases water loss and increases energy demand to some degree.

Carroll et al. (2015) discovered large temperature variations across their study area that provided unique microclimates affecting bobwhite behavior during the brood-rearing period. Hot microclimates can thermally fragment bobwhite habitat as the birds avoid areas with extremely high temperatures (Forrester et al. 1998, Guthery et al. 2000). We measured ground-level air temperatures (T_a) during the warm season to characterize this aspect of epigeal microclimates found in 4 habitat types (disked and nondisked native grass, disked and nondisked sericea). Our goal was to gain insight into how management practices affect T_a in our study area. Specifically, we wanted to know how much the presence–absence of sericea lespedeza would affect T_a. We also wanted to find out how much T_a was affected by whether areas had been disked or not because the surface microclimate becomes more extreme (i.e., higher maximum temperature and lower minimum temperature) with decreased vegetation soil covering and shading (Geiger et al. 2003).

Distler et al. (2015) predict that climate change will cause decreases in bird species richness in summer over much of North America, including Kentucky. Lusk et al. (2001) suggest that bobwhites may be able to adapt to increases in average temperature but caution that the pace at which climate change occurs may affect their resilience. They also state that bobwhites are particularly sensitive to high summer temperatures that exceed their ability to cope. Climate models predict that average temperatures in our study area will increase 2–3° C by the end of this century and days warmer than 32.2° C will become more common (USGCRP 2014). The warmer climate will exacerbate negative effects that excessive heat has on bobwhites at our study site. Current management practices there focus on removing sericea and providing more open space for birds. Although these actions provide appropriate substrate, they may also result in elevated local temperatures.

STUDY AREA

Our study site was a reclaimed surface mine; approximately 580 ha on the Sinclair tract of Peabody Wildlife Management Area in western Kentucky (hereafter, Peabody). Western Kentucky lies in the northern part of the humid subtropical climate zone of the southeastern United States. This is a transition zone just south of the humid continental climate of the US Midwest, which has much colder and longer winters than Kentucky. Maximum temperatures in the summer often exceed 32° C and occasionally rise above 38° C. Winter minimum temperatures rarely fall below –18° C. The highest ground-level air temperature observed at Peabody during our study period was 37.3° C. Average annual precipitation in western Kentucky measures 1,250 mm with no distinct wet or dry seasons. Precipitation during our study period was similar to long-term climatological averages for the region.

All vegetation and soil at Peabody was stripped during the mining process. The bedrock was subsequently covered with a thin layer of 'fill' of varying quality and thickness that was compacted by heavy equipment during reclamation. The resultant topography is relatively flat with elevations ranging from 122 m to 180 m. Land-use classification derived from satellite imagery showed the following: 57.4% open herbaceous, 19.7% scrub shrub, 9% native warm season grass, 5% water or emergent wetland, 4.2% deciduous forest, 2.2% firebreaks, 1.4% covered by roads or other development, and 1.1% used for annual grain production.

METHODS

Native grass and sericea lespedeza (the dominant nonnative species) are the primary nesting options at Peabody. However, given the limited value of serica as a nesting substrate, disking is regularly implemented as a management strategy. We divided the study area into sections having 4 different habitats (NG = native grass, DN = disked native grass, SL = sericea lespedeza, DS = disked sericea lespedeza; Fig. 1). Disking occurred approximately 3 years to 3 months prior to temperature-logger deployment, although the specific time since disking for any given location was unknown and therefore unfortunately not considered in this analysis. Thirty temperature loggers (Onset HOBO Pendant Temperature and Light Data Loggers; Onset Computer Corporation, Bourne, MA, USA) were randomized spatially in each habitat type and deployed at ground level beneath radiation shields. Shielding the instruments was necessary because the temperature loggers we used are incapable of obtaining accurate readings in direct sunlight. Loggers collected data at 10-minute intervals from 25 June through 30 September 2015. Previous research at Peabody

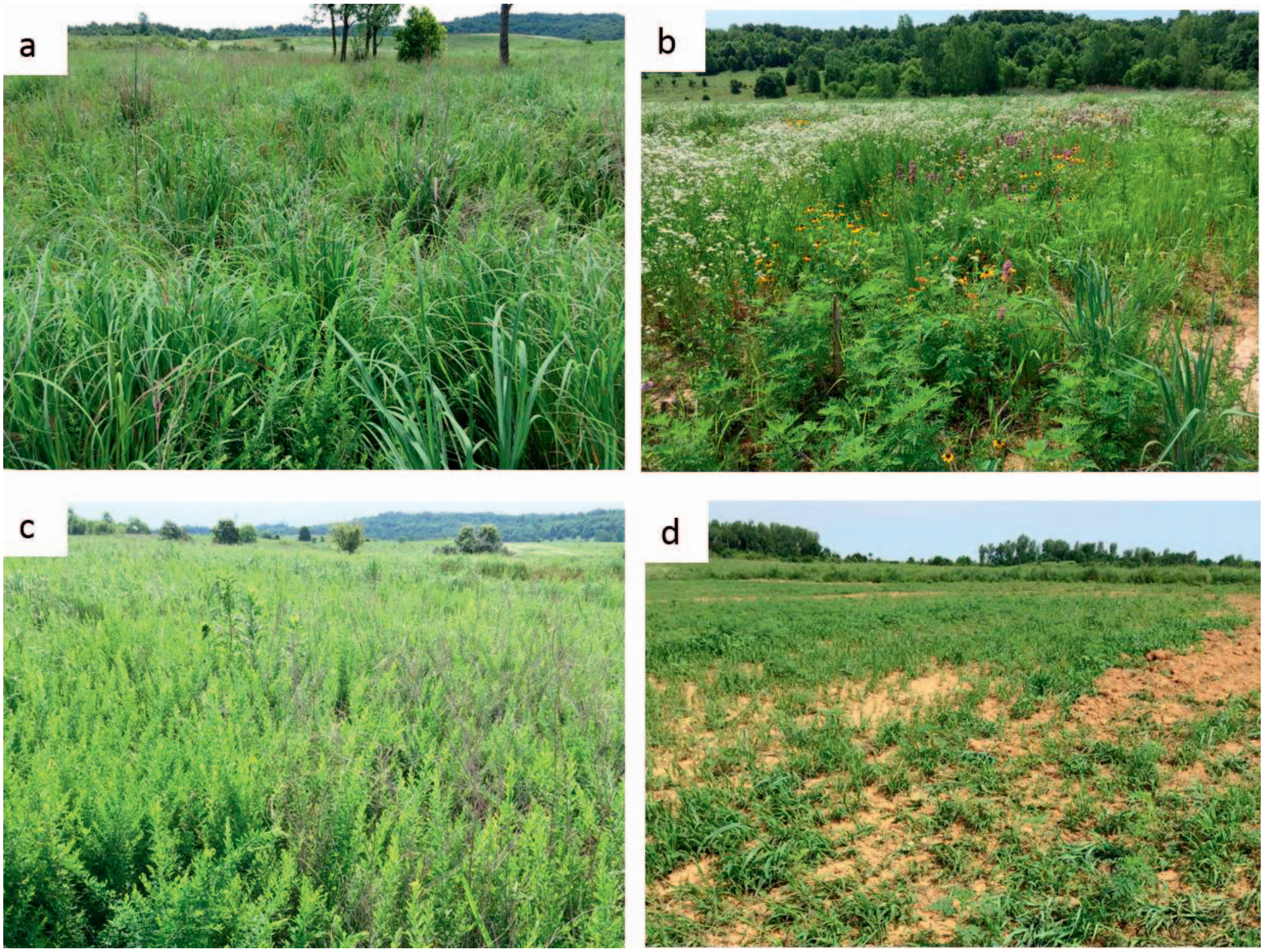

Fig. 1. Examples of each habitat type in northern bobwhite nesting habitat at Peabody Wildlife Management Area, Kentucky, USA (26 Jun–17 Jul 2015). a) native grass (NG), b) disked native grass (DN), c) sericea lespedeza (SL), d) disked sericea lespedeza (DS).

identified the peak nesting time period as 29 May through 3 July, and peak timing for chicks on the ground as 26 June through 17 July (Brooke 2015). We focused this analysis on data collected 26 June through 17 July to concentrate on peak brood-rearing. We removed suspect or biased data from consideration prior to data analysis (e.g., if a logger had been washed out from under its radiation shield during a storm). The final numbers of loggers with reliable data were NG = 28, DN = 30, SL = 27, DS = 25 (Fig. 2).

We assessed the habitat at each temperature logger location using established methods. We quantified percent ground cover of primary vegetation categories (Grass, Forb–Legume, Bare Ground, and Leaf Litter) using a 1-m × 1-m Daubenmire cover frame (Daubenmire 1959; Table 1). We used a vertical cover–profile board (Nudds 1977) to measure vegetation structure at each location. We measured litter depth (cm) at the plot center using a plastic ruler. We also recorded slope and orientation at each site. We computed correlation coefficients and coefficients of determination between air temperature and quantitative variables (e.g., percent vegetation cover, litter depth, and slope). We conducted one-way analysis of variance (ANOVA) tests to look for significant differences ($\alpha = 0.05$) in T_a between habitat types and slope aspect. We identified all observations >40° C based on Reyna and Burggren (2012), and those >35° C and >39° C based on Guthery et al. (2005).

RESULTS

Compared with nondisked areas, disked areas are generally more open, offering more bare ground for bird mobility. DN areas had an average of 25.3% more bare ground than NG; DS had an average of 34.2% more bare ground than SL (Table 1). These differences are significant at the 95% confidence level. Litter depth was significantly different ($\alpha = 0.05$) in each habitat type with SL having the greatest average followed by NG, DS, and DN with the least.

Percentages of various land covers (grass, forb, bare ground, and leaf litter) and leaf litter depth were moderately to weakly correlated with daily maximum and minimum temperatures (T_{max}, T_{min}); however, all

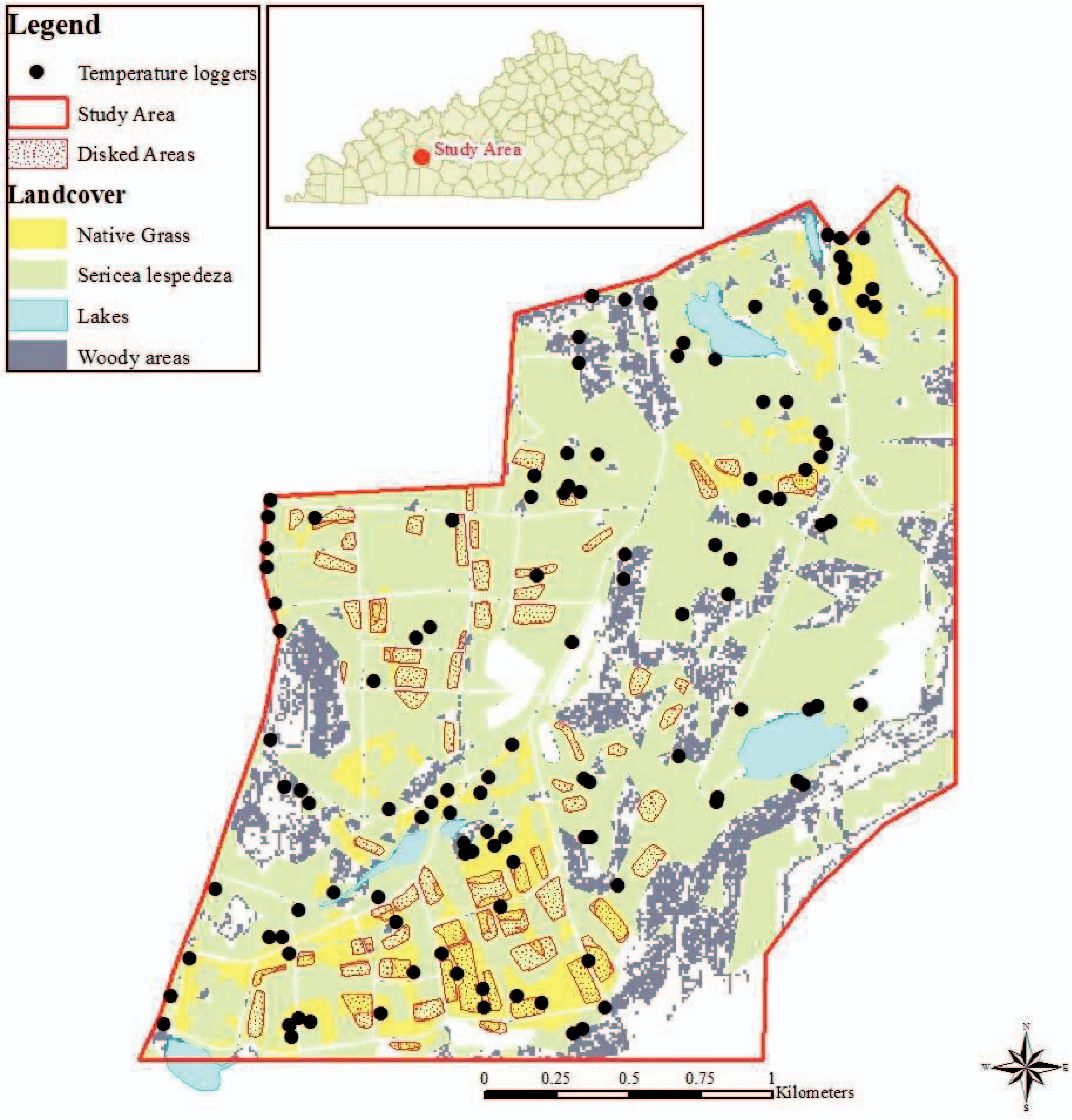

Fig. 2. Study area and temperature data logger locations (Sinclair tract of Peabody Wildlife Management Area, Muhlenberg County, KY, USA) within northern bobwhite nesting habitat, 26 June–17 July 2015. Native grass and sericea lespedeza (the dominant nonnative species) are the primary nesting options at Peabody. Managed areas were either left in their natural state (nondisked) or disked to provide more open space for bobwhites by removing excess vegetation.

correlations were statistically significant at the 95% confidence level (Table 2). The strongest positive correlation with daily temperatures occurred with percent bare ground, which explained 15.2% and 21.3% of the variation in daily T_{max} and T_{min}, respectively. Moreover, the highest maximum temperatures observed during our study occurred at locations with the highest percent of bare ground (Fig. 3). The strongest negative correlation with daily temperatures occurred with percent leaf litter, which explained 19.5% and 25.3% of the variation in daily T_{max} and T_{min}, respectively. A site's slope aspect could affect daily T_{max}. One-way ANOVA tests revealed that loggers located on west-facing slopes recorded significantly warmer daily T_{max} than loggers on all other slopes ($\alpha = 0.05$). T_{min} was not significantly affected by slope aspect.

Table 1. Summary of vegetation assessment of northern bobwhite nesting habitat at Peabody Wildlife Management Area, Kentucky, USA, conducted during 26 June–17 July 2015. Mean [SD])is reported for 4 habitat classifications (disked and nondisked native grass, disked and nondisked sericea). The percent ground cover of primary vegetation categories (Grass, Forb–Legume, Bare Ground, and Leaf Litter) was quantified using a 1-m × 1-m Daubenmire cover frame (Daubenmire 1959). Note: vegetation cover values of canopy (% grass and % forb or legume) and ground cover (% bare ground and % leaf litter) were estimated independently allowing for a total sum >100%. Disked areas had greater percentages of bare ground and less litter depth, allowing more sunlight to reach and warm the ground in those areas.

	% Grass	% Forb–Legume	% Bare ground	% Leaf litter	Litter depth (cm)
Disked native grass ($N = 30$)	29.0 [27.6]	64.3 [27.5]	41.8 [26.7]	37.5 [28.3]	0.6 [1.3]
Disked sericea ($N = 25$)	26.6 [31.4]	63.2 [26.6]	37.2 [24.6]	40.6 [32.1]	1.4 [1.8]
Native grass ($N = 28$)	57.1 [23.8]	33.6 [24.1]	17.0 [16.2]	63.8 [23.2]	2.6 [2.0]
Sericea ($N = 27$)	7.0 [11.8]	85.4 [11.2]	3.0 [4.8]	83.0 [7.6]	4.5 [2.8]

Differences in the average daily maximum and minimum temperatures between habitat types were small (Table 3). Disked areas were generally warmer and areas of nondisked sericea were coolest. Differences in average daily T_{max} and T_{min} were exceeded by the standard deviation within each habitat type but some differences were statistically significant. One-way ANOVA tests using habitat type as the factor showed that disked areas had significantly higher average daily T_{max} and T_{min} than nondisked areas ($\alpha = 0.05$). There was no significant difference between temperatures recorded in areas of disked native grass and disked sericea. Loggers in nondisked native grass recorded significantly higher T_{max} than nondisked sericea but there was no significant difference in T_{min} at nondisked sites.

Temperatures never reached the 39° C or 40° C thresholds during our study. $T_a > 35°$ C occurred 99 times during the study period (<0.03% of all 10-min observations). These events were concentrated during 5 days at 9 different observation sites. Eight of the 9 sites in this subset were disked. Eighty-two of the 99 $T_a > 35°$ C events happened at just 3 sites. All 3 sites were disked and had 60%, 80%, and 85% bare ground exposed. $T_a > 35°$ C events were not exclusive to freshly disked areas with ample bare ground, however, because temperatures exceeding 35° C were occasionally observed in areas having abundant grass and forb shading the ground (Fig. 4).

Table 2. Correlation coefficients (*r*) and coefficients of determination (r^2) between variables related to northern bobwhite nesting habitat site characteristics and daily maximum and minimum temperature (T_{max}, T_{min}) at Peabody Wildlife Management Area, Kentucky, USA (26 Jun–17 Jul 2015). All values are statistically significant at the 95% confidence level. Percent ground cover of primary vegetation categories (Grass, Forb–Legume, Bare Ground, and Leaf Litter) was quantified using a 1-m × 1-m Daubenmire cover frame (Daubenmire 1959). Percent bare ground had the strongest positive correlation, with both T_{max} and T_{min} indicating that warmer temperatures were observed in areas with increased amounts of bare ground. Percent leaf litter and litter depth were negatively correlated with T_{max} and T_{min}, suggesting that leaf litter had a cooling effect on temperatures near the ground. Slope, percent grass, and percent forb–legume all had very weak correlations with daily maximum and minimum temperature.

	Daily T_{max}		Daily T_{min}	
	r	r^2	*r*	r^2
Slope	−0.073	0.005	−0.188	0.035
% Grass	0.057	0.003	0.075	0.006
% Forb–legume	−0.174	0.030	−0.123	0.015
% Bare ground	0.389	0.152	0.462	0.213
% Leaf litter	−0.442	0.195	−0.503	0.253
Litter depth (cm)	−0.295	0.087	−0.425	0.181

DISCUSSION

Surface mining has scarred huge amounts of land that intensive management can transform into high-quality bobwhite habitat. Determining best management practices requires considering a myriad of factors, including microclimate. The highest ground-level temperature observed during our study period (37.3° C) was below the 40° C threshold that Reyna and Burggren (2012) reported as being fatal to bobwhite embryos and below the 39° C threshold that causes quail to become hyperthermic (Guthery et al. 2005). Some of our observations exceeded 35° C, which Guthery et al. (2005) found to initiate gular flutter in approximately 90% of incubating bobwhites. Although temperatures high enough to induce gular flutter occurred infrequently

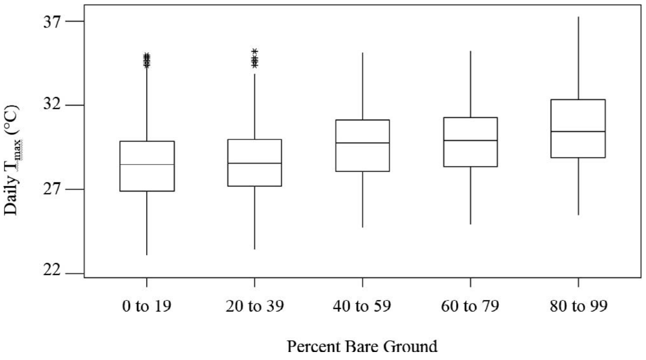

Fig. 3. Boxplots of daily maximum temperature and percentage of bare ground exposed at observation locations of northern bobwhite nesting habitat at Peabody Wildlife Management Area, Kentucky, USA (26 Jun–17 Jul 2015). Areas of sparse vegetation, including freshly disked areas, experience the highest maximum temperatures. This, combined with the lack of shade, means there is greater risk of bobwhite heat stress in areas having high percentages of bare ground.

Table 3. Daily maximum (T_{max}) and minimum (T_{min}) air temperature by northern bobwhite nesting habitat type (disked and nondisked native grass, disked and nondisked sericea) at Peabody Wildlife Management Area, Kentucky, USA (26 Jun–17 Jul 2015). Disked areas had higher daily maximum and minimum temperatures on average. The highest maximum temperature was observed in a disked native grass area.

	Daily T_{max} (° C)				Daily T_{min} (° C)			
	$\bar{x}$	SD	Hi	Low	$\bar{x}$	SD	Hi	Low
Disked native grass	29.66	2.20	37.27	24.55	22.48	1.81	26.59	15.47
Disked sericea	29.70	2.15	35.22	24.74	22.42	1.68	26.59	15.76
Native grass	28.46	2.30	35.22	23.48	21.71	1.76	26.49	14.71
Sericea	28.11	2.18	34.16	23.10	21.34	1.73	25.51	14.61

at Peabody during our study, extreme high temperatures are expected to become more common in the future (IPCC 2013). Climate models project that if global emissions of greenhouse gases continue to grow, summertime temperatures in the United States that ranked among the hottest 5% in 1950–1979 will occur ≥70% of the time by 2035–2064 (USGCRP 2014). Furthermore, our findings likely underestimated actual thermal load on bobwhites because temperature loggers were shielded from direct sunlight.

The largest factor affecting ground-level temperature variability in our study was whether or not an area had been disked. Disked areas were warmer than nondisked areas, which could be a concern in warmer areas and/or during hotter summers. Maximum and minimum daily temperatures were lowest in areas of SL, most likely on account of less direct sunlight reaching the surface (only 3% bare ground on average). Doxon and Carroll (2010) found that bare ground cover had a profound impact on bobwhite chick survival because it enhanced invertebrate availability and diversity, and chick mobility influenced feeding rates. Disking opens up areas of bare ground, which is necessary at Peabody because areas of NG and SL only had an average of 17% and 3% bare ground, respectively. Future work at Peabody should monitor the speed of regrowth following disking to help determine optimal intervals between habitat disturbances.

Fig. 4. Ground-level temperature of northern bobwhite nesting habitat at Peabody Wildlife Management Area, Kentucky, USA, which exceeded 35° C at this site located within disked native grass habitat 4 times during the study period (26 Jun–17 Jul 2015). This illustrates that thermal stress can be a concern for bobwhite in what otherwise appears to be a well-suited habitat (30% grass, 65% forb, 40% bare ground, and 20% leaf litter). The white square in lower right is the solar radiation shield protecting the temperature logger. Note that multiple thermal refuges are available nearby.

Greater vegetation nutrition was available for quail in disked areas than in areas of nondisked native grass given greater amounts and diversity of forbs and legumes present (>63% forb cover on average in disked areas compared with 33.6% in NG areas). It is possible that reducing sericea and increasing vegetation species diversity also aids in attracting insects (Blocksome 2006). This potential benefit has been enhanced in disked areas at Peabody through the successful seeding of plants such as bee-balm (*Monarda didyma*) and black-eyed Susan (*Rudbeckia hirta;* Fig. 1b). Accordingly, we recommend studies assessing the impact of disking on the biomass and diversity of bobwhite food sources.

None of the metrics we tested explained >19.5% of the variance in daily maximum temperature at ground level. Although increased vegetation cover should theoretically reduce daytime T_{max}, the percentage of bare ground alone did not reliably predict where thermal hot spots would occur in this reclaimed mine landscape. This suggests that the compacted subsurface geology in reclaimed mine sites can outweigh the effects vegetative forcing has on surface T_a. Future work on reclaimed surface mines should investigate how the spatial variability of soils affects microclimate and vegetation success.

Climate change will affect bobwhite populations in the future. Throughout much of the world, temperatures are expected to increase, growing seasons to lengthen, precipitation to become more variable and erratic, and droughts to become more severe (IPCC 2014). The magnitude of climatic changes and associated impacts depends on future greenhouse gas emissions and changes will also be different for different parts of the globe. Under all future emissions scenarios, however, the number of days with high temperatures >32.2° C is expected to increase throughout the United States, especially toward the end of this century (USGCRP 2014). Climate model runs produced for the Intergovernmental Panel on Climate Changes's 5th Assessment Report project temperatures in Kentucky to be 2–3° C warmer at the end of this century than they were at its beginning (IPCC 2013). Those same models predict a 0–20% increase in Kentucky's annual precipitation over the same period. Phenology changes and species distribution shifts will likely affect forage quality in Kentucky as species composition of pastures changes (Vincelli et al. 2011). Simulating warming (+3° C above ambient temperature) and increased precipitation (+30% long-term normal precipitation) over pasture in central Kentucky, McCulley et al. (2014) observed significant changes in plant species composition. Such changes could greatly affect bobwhite health, further exacerbating the need for habitat management. Climate change directly affects birds as well. Several bird species have experienced changes in breeding age, timing of migration, breeding performance (egg size, nesting success), population sizes, and population distributions (Crick 2004). As Kentucky's climate warms, microclimate will become increasingly important in habitat management. Several strategies have been proposed for conserving biodiversity that incorporate uncertainties associated with climate change (e.g., Burgman et al. 2005, Bagchi et al. 2013). Unfortunately, none of these approaches provide sufficient information to guide conservation decisions concerning specific species or communities. Management strategies incorporating climate change scenarios are needed for northern bobwhite conservation.

MANAGEMENT IMPLICATIONS

Our findings, coupled with future climate projections, underscore the importance of considering appropriate thermal climates when developing management strategies. Vegetation at Peabody tends to grow very densely, which degrades bobwhite habitat. Disking creates open space birds need but also results in higher air temperatures at ground level. The lack of shade in newly disked areas could stress birds. Disking should be focused on areas near existing thermal cover or thermal cover should be added to disked areas without it. Our discovery that excessive T_a can also occur in areas with little bare ground exposed advocates offering more thermal refuges throughout managed areas. Projected climatic warming will further increase the need for thermal cover. Climate models predict average temperature across Kentucky to increase 2–3° C over the next century. If these models are correct, temperature thresholds critical to bobwhite well-being will be exceeded regularly. Therefore, managers may want to consider microclimate and proximity to thermal refuges in addition to trade-offs in substrate (e.g., more grass vs. forbs, open canopy vs. closed) when contemplating management actions.

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VEGETATION AND ARTHROPOD RESPONSES TO BRUSH REDUCTION BY GRUBBING AND STACKING

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ABSTRACT

Grubbing is a mechanical brush-reduction technique that allows targeting of mesquite (*Prosopis glandulosa*) and huisache (*Vachellia farnesiana*) and can be used to open lanes for hunting northern bobwhites (*Colinus virginianus*). Follow-up treatments of stacking allow the piling up of downed brush. We initiated this study on the Santa Gertrudis Division of the King Ranch, Inc., Texas, to determine effects of grubbing and stacking on vegetation and arthropod communities important to bobwhite. We hypothesized that grubbing and stacking would be able to selectively remove mesquite and huisache while leaving mixed brush species largely intact. We hypothesized that soil disturbance treatments would lead to improved brooding, feeding, and nesting habitat for bobwhite through an increase in herbaceous food plants, arthropods, and nesting cover. We sampled vegetation prior to treatment during July 2012 and posttreatment during November 2012, March 2013, and July 2013. We sampled arthropods before treatment in July 2012 and monthly posttreatment until July 2013, a year marked by extreme drought in South Texas. We detected a positive response of bobwhite food grasses and/or sedges 1 year after initial treatments but detected no treatment effect on bobwhite food forbs. We detected no effects of treatments on nesting cover. Grubbing and stacking did not affect total Insecta abundance; however, Insecta biomass and Arachnida abundance and biomass responded both positively and negatively to treatments. To better understand the effects of grubbing and stacking, replication of this study during years of average and above average precipitation should be conducted.

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Key words: *Vachellia farnesiana,* Arthropoda, D-Vac, honey mesquite, huisache, grubbing, *Prosopis glandulosa,* stacking, sweep net

Woody-plant encroachment is common and widespread throughout rangelands in much of the United States (Van Auken 2000). Such encroachment could be caused by many factors including livestock grazing, changes in fire frequencies, and elevated levels of CO_2; such encroachment is likely a combination of many factors (Van Auken 2000). Smith and Rechenthin (1964) reported that 93% of the Rio Grande Plains and 34% of the Coastal Prairie in Texas have some brush infestation. This is not necessarily detrimental for northern bobwhite (*Colinus virginianus*), given that woody plants provide them with basic habitat resources (Stoddard 1931, Rosene 1969, Lehmann 1984, Schroeder 1985). Opinions vary on the ideal percentage of woody cover for bobwhites. Lyons and Ginnet (1998) suggest 15–25% woody cover of short stature, typically <1 m tall. In Wilbarger County, Texas, bobwhites selected areas that averaged 29% woody canopy cover (Ransom et al. 2008) but selected for areas of 20–60% woody cover and avoided areas with <20% in South Texas (Kopp et al. 1998). This illustrates that

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bobwhite often use areas with high percentage of brush cover at the landscape level. What further complicates these relationships is the concept of habitat slack (Guthery 1999), which postulates that different habitat configurations may be equally suitable for bobwhites. Tall herbaceous cover can partially take the place of woody cover by providing screening and loafing cover, and different amounts of woody cover may be equally inhabitable (Hernández and Guthery 2012).

Although woody cover is a crucial habitat component for bobwhites, woody plants can outcompete grasses and forbs that provide nesting cover and food for bobwhites (Guthery 1986, Hernández and Guthery 2012). As a result of this competition, excessive woody cover can limit the amount of usable habitat space available to bobwhites (Guthery 1999, Hernández and Guthery 2012). Brush management of thick stands can increase edge and interspersion of habitat types (Guthery and Rollins 1997) and reduce the competitive effect of woody plants on important grasses and forbs (Fulbright 1997). Soil disturbance through brush management also favors many species of bobwhite food forbs and grasses (Guthery 1986). However, although brush management may be beneficial in certain situations, food produced by herbaceous plants is often not a limiting factor for bobwhites (Guthery 1997). Therefore, a brush management technique that increases bobwhite food plants will not necessarily increase bobwhite numbers.

Arthropods provide an important food resource for bobwhites, particularly chicks and laying females. Insects help satisfy high protein requirements of growing chicks (Nestler 1940) and laying females have been shown to consume 2.3–4.0 times more invertebrates than nonlaying females (Harveson et al. 2004). Yates et al. (1995) documented that bobwhites selected areas with a greater abundance of arthropods for brooding habitat. In South Texas, arthropods may be important year round in the bobwhite diet. Insects made up the highest percentage of the bobwhite diet during a dry winter and the lowest during a period of average spring precipitation on King Ranch from 1949 through 1951 (Lehmann 1984). In southwestern Texas, arthropods were found in 100% of bobwhite and scaled quail (*Callipepla squamata*) crops collected during June and September, and in 96% of crops collected during autumn and winter (Campbell-Kissock et al. 1985).

Grubbing is a mechanical treatment for brush management that land managers can use to combat brush encroachment (Bontrager et al. 1979). Unlike some other methods of brush management (e.g., root-plowing or chaining), grubbing is an individual plant treatment that allows for selectively removing woody plants. After grubbing, individual plants are left in place but stacking can be used in combination with grubbing to pile up downed brush left from grubbing.

We tested 3 hypotheses: 1) grubbing and stacking will leave mixed brush species (woody cover excluding mesquite and huisache) largely intact while removing mesquite and huisache; 2) the soil disturbance related to grubbing and stacking will improve brooding and feeding habitat by increasing canopy coverage of food-producing forbs, grasses, and/or sedges, as well as forb species richness, bare ground, arthropod abundance and biomass, which are all resources that are important to growing chicks and adult bobwhite; and 3) grubbing and stacking will improve nesting habitat by increasing the number of suitable nesting clumps for breeding bobwhites.

STUDY AREA

This study was conducted on the Santa Gertrudis Division of King Ranch, Inc. near Kingsville, Texas in Kleberg County (27.30°N, 97.51°W). The grubber and stacker work totaled 1,456 ha on cleared strips. A nontreated site was established on a 650-ha section of a pasture located at a maximum of 8,567 m from the treated sites. The most common soil type on the study area was Palobia fine sandy loam (fine-loamy, mixed, active, hyperthermic Typic Natrustalfs; Natural Resources Conservation Service 2011). Common woody species on the study area included honey mesquite (*Prosopis glandulosa*), huisache (*Vachellia farnesiana*), brasil (*Condalia hookeri*), and granjeno (*Celtis ehrenbergiana*). Common forbs included palafoxia (*Palafoxia texana ambigua*), crotons (*Croton* spp.), and sidas (*Sida* spp.). Common native grasses include sandbur (*Cenchrus* spp.), hooded windmillgrass (*Chloris cucullata*), tanglehead (*Heteropogon contortus*), gramas (*Bouteloua* spp.), and threeawns (*Aristida* spp.). Common nonnative grasses include guinea grass (*Megathyrsus maximus*), Durban's crowsfoot (*Dactyloctenium aegyptium*), buffelgrass (*Cenchrus ciliaris*), Kleberg bluestem (*Dichanthium annulatum*) and other Old World bluestems (*Dicanthium* and *Bothriochloa* spp.). Prior to treatments, the nontreated site was more open than the treated sites because of more regrowth running mesquite, which was likely a result of historical management practices. Grazing consisted of a cow–calf grazing operation (King Ranch, Inc., personal communication). Stocking rate was 13.4 ha/animal unit in 2012 and 24.3 ha/animal unit in 2013 in the pasture with the nontreated site and 10.9 ha/animal unit in 2012 and 17.8 ha/animal unit in 2013 in the pasture with the treated site. Stocking rates were reduced in treated and untreated sites in 2012 to compensate for the effects of the drought on forage availability.

Weather

Precipitation data were obtained from King Ranch, Inc. from a rain gauge 4,612 m from the farthest treated transect post and 3,970 m from the farthest nontreated transect post. Rain gauges were checked after each rain event by ranch personnel. Total precipitation was 46.5 cm during the study (Aug 2012–Jun 2013), far drier than the average annual precipitation of 65.5 cm from 1985 to 2012 on the Santa Gertrudis Division (King Ranch, Inc., personal communication). September 2012 and June 2013 had the most precipitation with 13.08 and 10.16 cm, respectively. October and December 2012, and March 2013, had no measurable precipitation (King Ranch, Inc.,

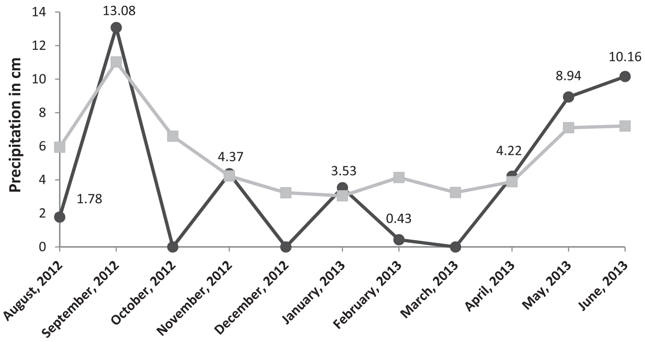

Fig. 1. Precipitation data obtained from King Ranch, Inc. The blue line represents the observed precipitation from August 2012 to June 2013 recorded at the Canelo Pens rain gauge (located between the treated and nontreated sites). Observed monthly precipitation totals included. The gray line represents the long-term monthly average over the entire Santa Gertrudis Division of the King Ranch, Inc., from 1985 to 2012 (Kleberg County, TX, USA).

personal communication; Fig. 1; Appendix A.). This study took place during an extreme drought.

METHODS

Study Design

Grubber work was completed in 10 seismic strips beginning in early August 2012. Seismic strips are cleared strips in a grid system used for oil and gas exploration. A Komatsu (Komatsu American Corp., Rolling Meadows, IL, USA) excavator was used to clear a width of 50-m strips on both sides of the seismic strips. The treatments were applied by the ranch and did not follow a systematic approach, but did follow treatment guidelines. The grubber operator targeted small to medium-sized (≤3 to ~5-m) honey mesquite and huisache and attempted to leave the mixed brush species intact. If there was no mixed brush around, one or two large mesquite or huisache were left intact to provide some shade and/or loafing cover. During November–December 2012, a stacker was used to push all the downed brush into piles along strips that had previously been grubbed. Brush piles were burned within 1 month of stacking. The main purpose of treatments was to clear brush and create strips to provide quail hunters access to areas that were too brushy to hunt effectively. However, treatments also were applied with the hope of improving bobwhite brooding, feeding, and nesting habitat.

Ten, 25-m permanent transects were established on the treated and nontreated site. On the treated site, transects were placed randomly within 5–40 m from the seismic strips, so that they were located in the treated site and not in the seismic strip itself. On the nontreated site, we limited transects to 300 m within the interior of the designated site and within 5–40 m of dirt roads to make it comparable to the treated site. Within these restrictions, permanent transects were placed randomly using Geographic Information System (ESRI, Redlands, CA, USA)

Vegetation Sampling

The percentage canopy cover of woody plants was measured using the line intercept-method (Canfield 1941). We measured the combined absolute canopy coverage of mesquite and huisache, as well as the combined absolute canopy of mixed brush (woody cover excluding mesquite and huisache) species. We measured availability of nesting cover by the number of suitable nest clumps that occurred within a plot of a 4-m-diameter circle, with the center of the circle occurring at the start and end of each transect. The 2 circles were added to obtain the total nesting clumps within an area of 6.28 m^2 at each transect. We described a suitable nest clump as a bunchgrass clump or multiple smaller clumps growing together with a base of ≥22.9 × 22.9 cm and a height of ≥22.9 cm (Lehmann 1984). We set the maximum number of clumps in the circle to 10 (20/6.28 m^2 at each transect) because of the difficulty of reliably counting clumps at higher densities than this. We used a 20 × 50-cm quadrat placed every meter along the permanent transect for 25 total quadrats/transect. We placed the quadrat randomly on the right or left of the transect at a distance of 0.5, 1.0, 1.5, or 2.0 m (Alvarez 2011). We used quadrats to estimate percent canopy cover of bare ground, bobwhite food forbs, and bobwhite food grasses and/or sedges. We estimated percent canopy cover to the nearest percent if it was between 1% and 10% and to the nearest 5% if it was >10%. We considered a dicot to be a bobwhite food forb if it was 1) a croton or legume (Guthery 1986), 2) listed in Larson et al. (2010) as a bobwhite food forb, and/or 3) listed as a bobwhite, scaled quail, or passerine bird food in Everitt et al. (1999). We considered a monocot to be a bobwhite food grass and/or sedge if it was a *Cenchrus, Panicum, Paspalum, Scleria, Setaria,* or *Urochloa* (Larson et al. 2010) excluding liverseed grass (*Urochloa panicoides*), an invasive grass species. We determined forb species richness at each transect by the number of species of broad leafed plants found in 25 quadrats. We collected vegetation data prior to treatments in July 2012 and posttreatment in November 2012, March 2013, and July 2013.

Arthropod Sampling

We used 2 methods to sample a more representative assemblage of the arthropod community (Buffington and Redak 1998, Standen 2000, Moir et al. 2005). Sweep-net and D-Vac sampling provide a more accurate representation of the taxonomic assemblage of arthropods than using only one method (Buffington and Redak 1998). Although there is some overlap in catch, the 2 methods differ in arthropods sampled by favoring different sizes and taxa (Buffington and Redak 1998, Doxon et al. 2011). This combination of sampling techniques allowed us to quantify several insect orders important in the bobwhite diet in South Texas, such as Coleoptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera (Lehmann 1984, Campbell-Kissock et al. 1985). We used a 39.4-cm sweep net of muslin cloth and a D-Vac Vacuum Insect Net Model 122 (D-Vac Sales Inc., Massapequa, NY, USA), with a 10.2-cm converter on the end (converter was included with the D-Vac) for sampling (Rincon-Vitova Insectaries, Ventura, CA, USA). With the sweep net, we walked 25 m, 4 paces to the right of the transect. We averaged 35 sweeps/transect with each sweep just above ground level. Then at a slow pace we walked back the length of the transect 4 paces to the right of the other side of the transect with the D-Vac on full throttle. We used 8 paces between sampling paths to avoid affecting one sampling method with the other while still sampling a path with a similar vegetation composition. Both sweep-net samples and D-Vac samples were collected within 1 minute for each transect. The same person sampled each time to avoid differences in pace and sampling technique between researchers. While sampling, we held the opening of the vacuum just above soil level except when going over thick vegetation. If brush was too dense to walk through with the sweep net or D-Vac, we walked around while staying as close to the line as possible. After sampling, we transferred arthropods to a plastic bag with cotton balls soaked in ethyl acetate and then froze them. In the lab, we sorted and counted arthropods. We sorted arthropods to class, and we sorted class Insecta to order. After sorting, we dried the samples for 24 hours at 105–110° C and weighed them to obtain biomass estimates for classes Arachnida and Insecta

We estimated abundance and biomass for classes Arachnida and Insecta prior to treatment in July 2012, and monthly following treatments through July 2013, with the exception of August and December 2012 because of the mechanical treatment application during these months. We began sampling around sunrise unless the herbaceous vegetation was wet or the temperature was below 7.5° C, in which case we started once the vegetation dried and the temperature increased. We began and ended sampling at the same transects every month, starting with the 10 treated transects and then moving to the 10 nontreated transects.

STATISTICAL ANALYSIS

Design Considerations

The treated and nontreated sites served as experimental units. We averaged all vegetation data collected for each transect and combined arthropod samples collected using both sweep nets and the D-Vac for each transect. In each site (treated and nontreated), we sampled 10 transects with sampling time analyzed as a repeated-measures effect. Treatments were not replicated; therefore, we estimated within-treatment variation with transect-to-transect variation, and thus inferences are limited to the particular experimental units in this study (Wester 1992). We combined data from treated and nontreated sites in a single analysis following Kempthorne (1952) with a statistical model that included 1) treatment as a main plot factor, 2) transect nested within treatment as a random effect used as an error term for the treatment effect (see above), 3) date and the interaction between treatment and date as subplot (repeated measures) effects, and 4) the crossed interaction between date and plot nested within treatment as the error term for date and its interaction with treatment.

Analysis Considerations

Residuals were nonnormally distributed and heteroscedastic; therefore, we analyzed all response variables with PERMANOVA+ (Anderson et al. 2008) using the model described above. For each dependent variable, if treatments differed ($P < 0.10$) for pretreatment data, we used analysis of covariance (ANCOVA) with pretreatment values as a covariable; otherwise, we used analysis of variance (ANOVA). For vegetation variables we analyzed, mesquite and huisache canopy cover, mixed brush canopy cover, forb species richness, and nesting clump density with ANOVA, while we used ANCOVA for bobwhite food grasses and/or sedges canopy, canopy cover of bobwhite food forbs, and bare ground cover. For the arthropod variables, we analyzed abundance and biomass of class Arachnida and class Insecta with ANOVA. We selected an alpha of 0.10 as the significance level because of high variation of arthropod variables. We tested treatment × date interactions first, and if there was an interaction ($P \leq 0.10$) treatment effects within dates were tested; if we detected no interaction ($P > 0.10$), we tested main effects of treatment (grubbing and stacking) and date, followed by a protected least significant difference test when appropriate (Kirk 2013). We used 10,000 permutations for all analyses.

RESULTS

Effects on Woody Cover

Differences between treatments depended on date for both mesquite and huisache cover ($P < 0.001$, $F_{3,54} = 10.518$) and mixed brush cover ($P < 0.001$, $F_{3,54} = 7.102$). Mesquite and huisache cover did not differ prior to treatments in July 2012 ($P = 0.289$, $F_{1,18} = 1.265$). Mesquite and huisache cover was 10.99% lower on the treated site 3 months after grubbing in November 2012 and approximately 12.4% and 14.72% ($P = 0.03$, $F_{1,18} = 6.955$) lower on treated sites following stacking in March ($P = 0.084$, $F_{1,18} = 3.759$) and July 2013 ($P = 0.052$, $F_{1,18} = 5.128$; Fig. 2). Mixed brush cover did not differ prior to treatments in July 2012 ($P = 0.888$, $F_{1,18} = 0.433$). Mixed brush cover was 6.48% lower on the treated site than the nontreated site 3 months after grubbing treatments in November 2012 ($P = 0.043$, $F_{1,18} = 5.346$), and it was 7.1% lower 3 months after stacking in March 2013 ($P = 0.037$, $F_{1,18} = 6.276$) and 8.96% lower 7 months after stacking in July 2013 ($P = 0.036$, $F_{1,18} = 5.913$; Fig. 3).

Herbaceous Response

Differences of treatment for bare ground depended on date ($P < 0.001$, $F_{2,36} = 10.37$) and the adjusted mean was >22.22% greater on the treated site than the nontreated site 3 months after stacking in March 2013 ($P = 0.086$, $F_{1,17} = 3.836$; 49.25% ± 3.41% on the treated site compared with 27.03% ± 3.41% on the nontreated site). Bare ground

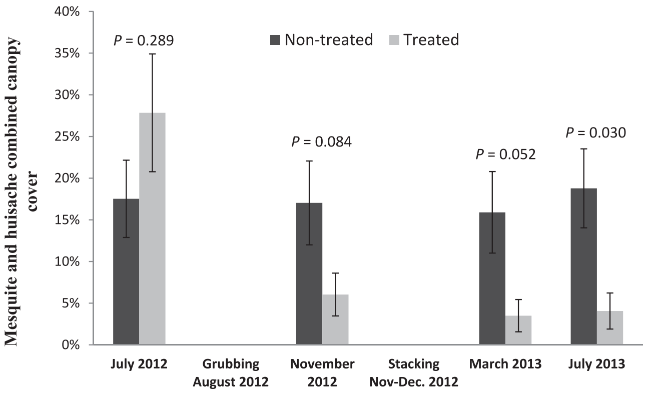

Fig. 2. Mesquite and huisache absolute combined canopy cover (Mean ± SE) estimated on 10 permanent transects using the line-intercept method. Treated represents grubbed and stacked sites and nontreated represents nontreated sites on the Santa Gertrudis Division of King Ranch, Inc. (Kleberg County, TX, USA). *P*-values obtained by analysis of variance tests of treatment effects within date. Treatment × date ($F = 10.518$), treatment within date effects: July 2012 ($F = 1.265$), November 2012 ($F = 3.759$), March 2013 ($F = 5.128$), July 2013 ($F = 6.955$).

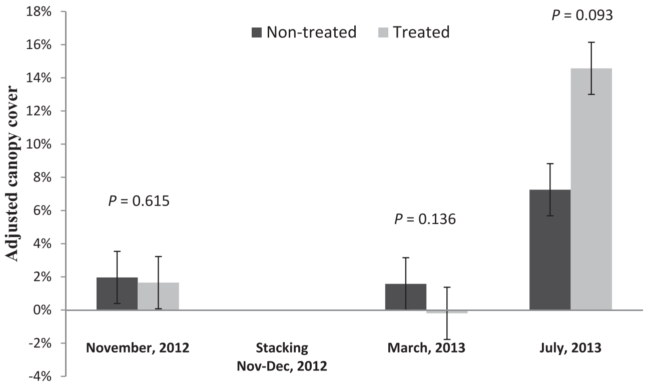

Fig. 4. Adjusted bobwhite food grasses and/or sedges canopy coverage (Mean ± SE) estimated on 10 permanent transects using 25 quadrats/transect. Canopy coverage adjusted because of the use of analysis of covariance. Treated represents grubbed and stacked sites and nontreated represents nontreated sites on the Santa Gertrudis Division of King Ranch, Inc. (Kleberg County, TX, USA). *P*-values obtained by analysis of covariance tests of treatment effects within date. Treatment × date ($F = 5.5023$), treatment within date effects: November 2012 ($F = 0.277$), March 2013 ($F = 2.729$), July 2013 ($F = 3.729$).

cover was not different between treatments 3 months after grubbing in November 2012 ($P = 0.441$, $F_{1,17} = 0.634$) and 7 months after stacking in July 2013 ($P = 0.44$, $F_{1,17} = 0.638$). Differences in treatments of forb species richness depended on date ($P < 0.001$, $F_{3,54} = 8.048$). Forb species richness did not differ prior to treatment in July 2012 ($P = 0.214$, $F_{1,18} = 1.794$). Forb species richness was 4.7 species greater in the treated site 3 months after stacking in March 2013 ($P = 0.005$, $F_{1,18} = 13.608$) but was not different 3 months after grubbing in November 2012 ($P = 0.473$, $F_{1,18} = 0.574$) and 7 months after stacking in July 2013 ($P = 0.941$, $F_{1,18} = 0.016$; Table 1). We did not detect an effect of treatment ($P = 0.256$, $F_{1,17} = 1.482$) or a treatment × date interaction on canopy cover of bobwhite food forbs ($P = 0.106$, $F_{2,36} = 2.388$; Table 1). There was a date effect on canopy cover of bobwhite food forbs ($P < 0.001$, $F_{2,36} = 42.116$): cover ranged from 2.86% ± 0.65% in March 2013 to 22.00% ± 1.59% in July 2013. Differences of treatments for bobwhite food grasses and/or sedges depended on date ($P = 0.008$, $F_{2,36} = 5.502$), and adjusted canopy coverage was 7.32% greater in the treated site 7 months after stacking in July 2013 ($P = 0.093$, $F_{1,17} = 3.729$), but did not differ 3 months after grubbing in November 2012 ($P = 0.615$, $F_{1,17} = 0.277$) or 3 months after stacking in March 2013 ($P = 0.136$, $F_{1,17} = 2.729$; Table 1; Fig. 4). We did not detect a treatment effect ($P = 0.245$, $F_{1,18} = 1.551$) or treatment × date interaction ($P = 0.249$, $F_{3,54} = 1.405$) on the number of nesting clumps, but the number of nesting clumps changed with date ($P < 0.001$, $F_{3,54} = 7.583$). We measured the lowest density of nesting clumps in March 2013 and the highest density of nesting clumps in July 2013.

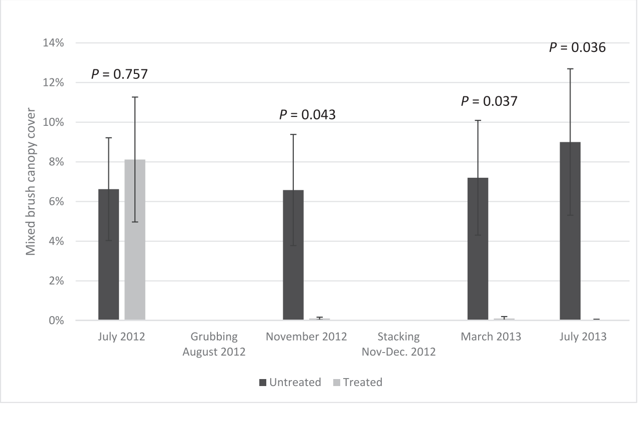

Fig. 3. Mixed brush absolute combined canopy cover (Mean ± SE) estimated on 10 permanent transects using the line-intercept method. Treated represents grubbed and stacked sites and nontreated represents nontreated sites on the Santa Gertrudis Division of King Ranch, Inc. (Kleberg County, TX, USA). *P*-values obtained by analysis of variance tests of treatment effects within date. Treatment × date ($F = 7.102$), treatment within date effects: July 2012 ($F = 0.096$), November 2012 ($F = 5.346$), March 2013 ($F = 6.276$), July 2013 ($F = 5.913$).

Arthropod Response

We collected 6,736 arthropods in the grubbed and stacked site and in the nontreated site from 11 months of sampling. Samples consisted of 2 classes of Arthropoda and 12 orders of Insecta (Table 2). Differences in Arachnida abundance between treatments depended on date ($P < 0.001$, $F_{10,180} = 4.814$): for example, abundance was 10 individuals/transect lower on the treated sites 1 month after grubbing in September 2012 ($P < 0.001$, $F_{1,18} = 25.568$) and 7.1 individuals/transect lower 1 month after stacking in January 2013 ($P = 0.039$, $F_{1,18} = 5.679$), but we detected no difference in the other 9 months ($P \geq 0.116$, $F_{1,18} \leq 2.928$; Table 3; Fig. 5). Differences in treatments in Arachnida biomass also depended on date ($P = 0.07$, $F_{10,180} = 1.722$), and Arachnida biomass was

Table 1. Summary of vegetation results[a] following grubbing and stacking on the Santa Gertrudis Division of King Ranch, Inc. (Kleberg County, TX, USA). We used analysis of variance unless treatments were different ($P < 0.10$) for pretreatment values, in which case we used analysis of covariance with pretreatment values as the covariable. We tested treatment × date interactions first and, if there was an interaction ($P \leq 0.100$), treatment effects within dates were tested. If no interaction was detected ($P > 0.100$), main (treatment and date) effects were tested. Ten thousand permutations were used for all analyses.

Response variable	Grubbing Aug 2012	Nov 2012	Stacking Nov–Dec 2012	Mar 2013	Jul 2013
Bare ground		ND		+	ND
Forb species richness		ND		+	ND
Food forbs canopy		No treatment effect or Treatment × date interaction ($P \geq 0.106$)			
Food grasses and/or Sedges canopy		ND		ND	+
Nesting clumps		No treatment effect or Treatment × date interaction ($P \geq 0.245$)			

[a] + if grubbed and stacked site was greater than nontreated site ($P \leq 0.100$), and ND if there was no difference ($P > 0.100$).

0.007 g/transect lower on the treated site 1 month after grubbing in September 2012 ($P = 0.032$, $F_{1,18} = 6.70$) 3 as well as 0.011 g/transect and 0.024 g/transect higher on the treated site 6 and 7 months after stacking in June ($P = 0.061$, $F_{1,18} = 4.618$) and July 2013 ($P = 0.066$, $F_{1,18} = 4.412$). We detected no difference in the other sampling months ($P \geq 0.296$, $F_{1,18} \leq 1.281$) but January 2013 was just below the alpha cut-off ($P = 0.101$, $F_{1,18} = 3.016$; Table 3; Fig. 6). We detected no effect of treatment ($P = 0.504$, $F_{1,18} = 0.486$) or treatment × date interaction ($P = 0.372$, $F_{10,180} = 1.092$) on Insecta abundance (Table 3) but there was a date effect ($P < 0.001$, $F_{10,180} = 22.814$) on Insecta abundance ($P < 0.001$). Insecta abundance ranged from 3.95 ± 0.56 individuals/transect in April 2013 to 75.7 ± 8.78 individuals/transect in October 2012. Difference of treatments for Insecta biomass depended on date ($P = 0.002$, $F_{10,180} = 3.002$). Insecta biomass was 0.139 g/transect lower on the treated sites 1 month after grubbing in September 2012 ($P = 0.029$, $F_{1,18} = 6.36$) but 0.345 g/transect higher on the treated site than the nontreated site 2 months after grubbing in October 2012 ($P = 0.079$, $F_{1,18} = 3.934$). Insecta biomass was also lower on the treated site 1, 2, 4, and 5 months after stacking in January ($P = 0.066$, $F_{1,18} = 4.444$), February ($P = 0.09$, $F_{1,18} = 3.548$), April ($P = 0.088$, $F_{1,18} =$), and May 2013 ($P = 0.054$, $F_{1,18} = 4.875$). We detected no difference in Insecta biomass in the other 5 sampling months ($P \geq 0.119$, $F_{1,18} \leq 2.867$; Table 3; Fig. 7).

Table 2. Summary of number of arthropods collected during 11 sampling months on treated site and nontreated site on the Santa Gertrudis Division of King Ranch, Inc. (Kleberg County, TX, USA). Samples collected with sweep net and D-Vac were pooled.

Order	No.
Arthropoda	6,736
Unknown	137
Arachnida	858
Insecta	5,741
Coleoptera	1,749
Hemiptera	1,449
Hymenoptera	587
Lepidoptera	293
Orthoptera	1,195
Other	468

DISCUSSION

Impacts on Woody Cover

Contrary to our initial hypothesis, grubbing and stacking did not leave mixed brush species intact but led to significant decreases in mixed brush cover. It should be noted that mixed brush was not eradicated on the study area even though it decreased on the permanent transects. Mesquite serves as a nursery plant for many species of woody plants (Archer et al. 1988). This association of mixed brush species with mesquite may make it difficult to remove one without damaging the other. Canopy coverage of brush following treatment on the treated strips was lower than bobwhite typically prefer to use (Kopp et al. 1998, Ransom et al. 2008); however, because of the strip treatment applications denser woody cover was available nearby.

Arthropod Response

We saw some positive responses from the arthropod community, as we hypothesized; however, contrary to what we expected, this positive response was short-lived and somewhat unpredictable. Contrary to what we hypothesized, we also saw negative responses for arthropod variables. However, these negative effects also appeared to be short-lived because variables returned to control levels or exceeded control levels the next month, with the exception of Insecta biomass, which remained lower in the treated site 2, 4, and 5 months poststacking. These quick rebounds of both abundance and biomass may be a result of the resiliency of the arthropod community. One potential limitation in a study like this is that weather and times of day are factors that have been shown to affect results obtained by sweep-net sampling (DeLong 1932, Romney 1945, Hughes 1955, Dumas et al. 1962).

Brooding, Feeding and Nesting Habitat

As we hypothesized, we detected some increases in canopy cover of bobwhite foods, forb species richness, and bare ground, which are resources that are important for brooding and feeding habitat. However, the results were mixed and, for many variables measured, the treatments did not have any effects. It should be noted that although the treated site had more bare ground cover

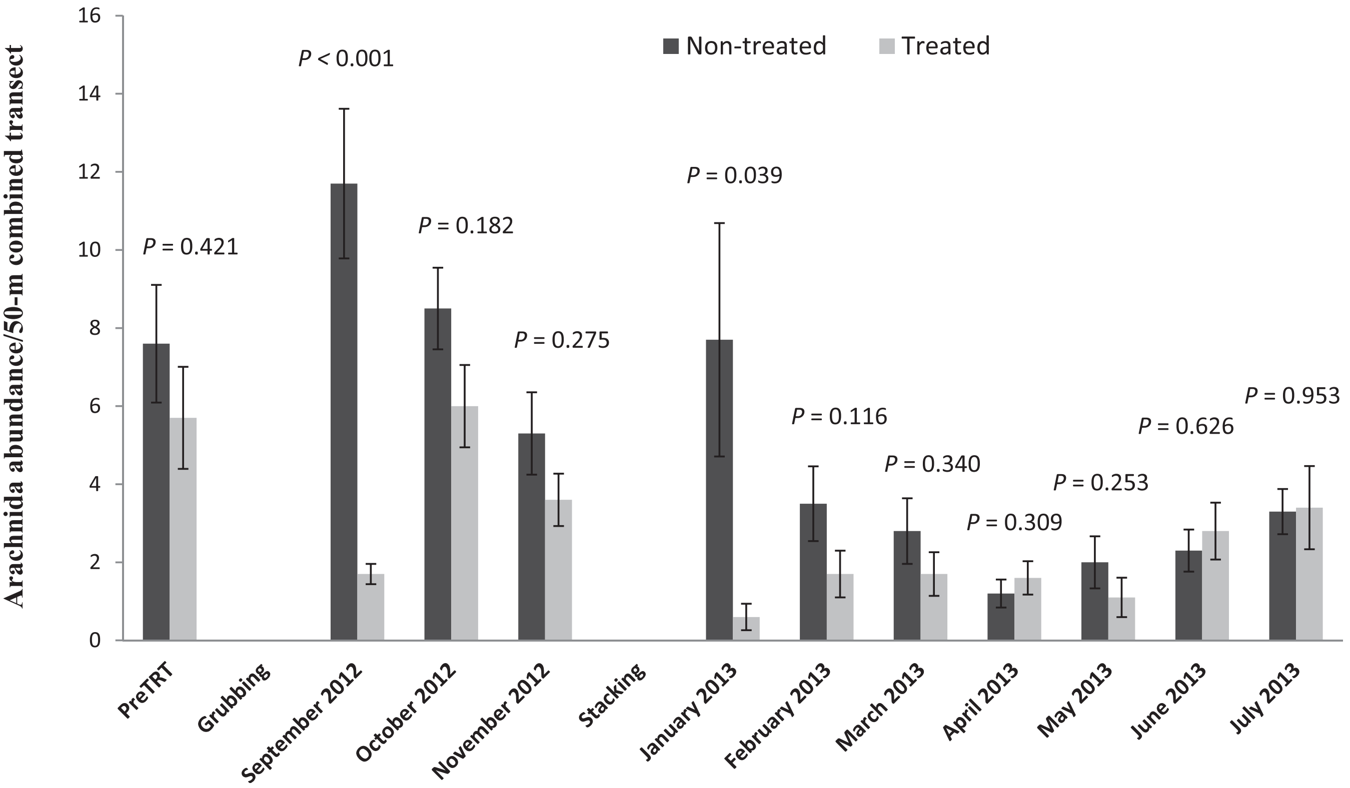

Fig. 5. Arachnida abundance (Mean ± SE)/50-m combined transect (25-m sampled with a sweep net and 25-m sampled with a D-Vac on 10 transects in each site). Treated represents grubbed and stacked sites and nontreated represents nontreated sites on the Santa Gertrudis Division of King Ranch, Inc. (Kleberg County, TX, USA). *P*-values obtained by analysis of variance tests of treatment effects within date. Treatment × date ($F = 4.814$), treatment within date effects: July 2012 ($F = 0.697$), September 2012 ($F = 25.568$), October 2012 ($F = 2.111$), November 2012 ($F = 1.34$), January 2013 ($F = 5.679$), February 2013 ($F = 2.928$), March 2013 ($F = 0.948$), April 2013 ($F = 1.161$), May 2013 ($F = 1.554$), June 2013 ($F = 0.26$), July 2013 ($F = 0.006$).

than the nontreated site in March 2013, this increase in bare ground cover may not have led to improved brooding habitat because both sites fell within the recommended range (Schroeder 1985, Guthery 1986). Contrary to what we hypothesized, we did not observe improved nesting habitat through increased nesting clump density following treatments. Although grubbing did not have an overall positive effect on many variables it did not appear to have much of a negative effect on bobwhite habitat and food sources either. Both vegetation and arthropod response variables rebounded to control levels quickly. This was the case even though the area was in a severe drought. Even during drought conditions, the treatments appeared to have only minor short-term negative effects and some positive effects.

Although we saw some positive and some negative responses, for most variables in the majority of months we detected no difference between treated and nontreated. The overall neutral effects we documented are not uncommon in semiarid environments. Habitat, arthropods, and bobwhite populations tend to respond positively to treatments in mesic environments (Stoddard 1931, Hurst 1971, Cram et al. 2002, Yarrow et al. 2009). However, the response in more xeric environments is much less

Table 3. Summary of arthropod results[a] following grubbing and stacking on the Santa Gertrudis Division of King Ranch, Inc. (Kleberg County, TX, USA). We used analysis of variance for the analysis unless treatments were different ($P < 0.10$) for pretreatment values, in which case we used analysis of covariance with pretreatment values as the covariable. We tested treatment × date interactions first and, if there was an interaction ($P \leq 0.100$), treatment effects within dates were tested. If no interaction was detected ($P > 0.100$), main (treatment and date) effects were tested. Ten thousand permutations were used for all analyses.

Response variable	Grubbing	Sep 2012	Oct 2012	Nov 2012	Stacking	Jan 2013	Feb 2013	Mar 2013	Apr 2013	May 2013	Jun 2013	Jul 2013
Arach. abundance		–	ND	ND		–	ND	ND	ND	ND	ND	ND
Arach. biomass		–	ND	ND		ND	ND	ND	ND	ND	+	+
Insecta abundance				No treatment effect or Treatment × Date interaction ($P \geq 0.372$)								
Insecta biomass		–	+	ND		–	–	ND	–	–	ND	ND

[a] + if grubbed and stacked site was greater than nontreated site ($P \leq 0.100$), – if nontreated site was greater than grubbed and stacked site ($P \leq 0.100$), and ND if there was no difference ($P > 0.100$).

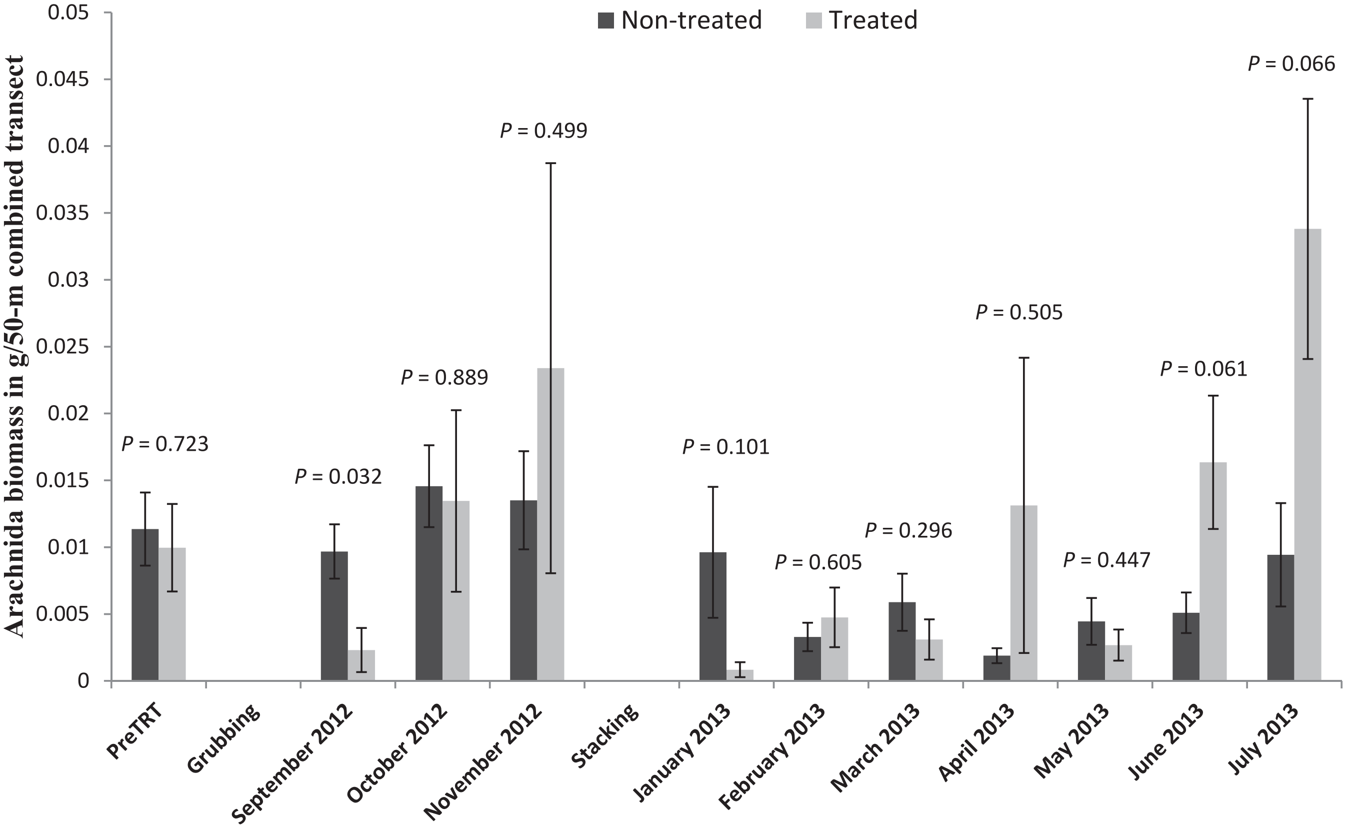

Fig. 6. Arachnida biomass (Mean ± SE)/50-m combined transect (25-m sampled with a sweep net and 25-m sampled with a D-Vac on 10 transects in each site). Treated represents grubbed and stacked sites and nontreated represents nontreated sites on the Santa Gertrudis Division of King Ranch, Inc. (Kleberg County, TX, USA). *P*-values obtained by analysis of variance tests of treatment effects within date. Treatment × date ($F = 1.722$), treatment within date effects: July 2012 ($F = 0.135$), September 2012 ($F = 6.7$), October 2012 ($F = 0.017$), November 2012 ($F = 0.523$), January 2013 ($F = 3.016$), February 2013 ($F = 0.3$), March 2013 ($F = 1.281$), April 2013 ($F = 1.011$), May 2013 ($F = 0.669$), June 2013 ($F = 4.618$), July 2013 ($F = 4.412$).

predictable (Wilson and Crawford 1979, Kane 1988, Leif 1993, Rollins and Lyons 2009) and largely dependent on rainfall (Bozzo et al. 1992). As site productivity decreases, optimal seral stage for bobwhites may increase (Spears et al. 1993). In some sites, mid- to late-seral stage may be better habitat for bobwhites (Hernández and Guthery 2012). If this is the case, habitat management practices that set back seral stage in sites with low productivity would likely have a neutral or negative effect as opposed to the predictable positive response in mesic areas.

Our conclusions are constrained in 2 senses: we lacked spatial replication (because of the logistic difficulties of replicating experimental units that exceeded 650 ha) and temporal replication. This study was also conducted during a historic drought and results should be interpreted with that in mind. Replication of this study during years of average and above-average precipitation should be conducted to better understand the effects of grubbing and stacking on the herbaceous and arthropod communities important to northern bobwhite. We also did not have control over grazing or past management practices on our 2 study sites, both of which likely affected our results. Heavier grazing in the untreated site during the study may have promoted early successional grasses and forbs, as well arthropods (Guthery 1986), which may have affected our results.

MANAGEMENT IMPLICATIONS

The combination of grubbing and stacking is a management tool that can drastically decrease brush cover and open up the area while showing greater selectivity than some other mechanical methods. However, it is quite expensive, because management costs averaged $444.79/ha for this brush management application (King Ranch, Inc., personal communication).

The main benefit of grubbing, in comparison with other brush management treatments, is the ability to leave mixed brush species intact while being able to selectively remove problem species. The association of mixed brush with mesquite on South Texas rangelands may make it difficult for the grubber operator to remove mesquite without unintentionally damaging or removing mixed brush. Operators should be well-trained in identifying woody species and able to carefully remove the mesquite or huisache without damaging mixed brush. If an operator is unable to do this efficiently, it may be far more cost-effective to use a cheaper, less selective practice of brush management.

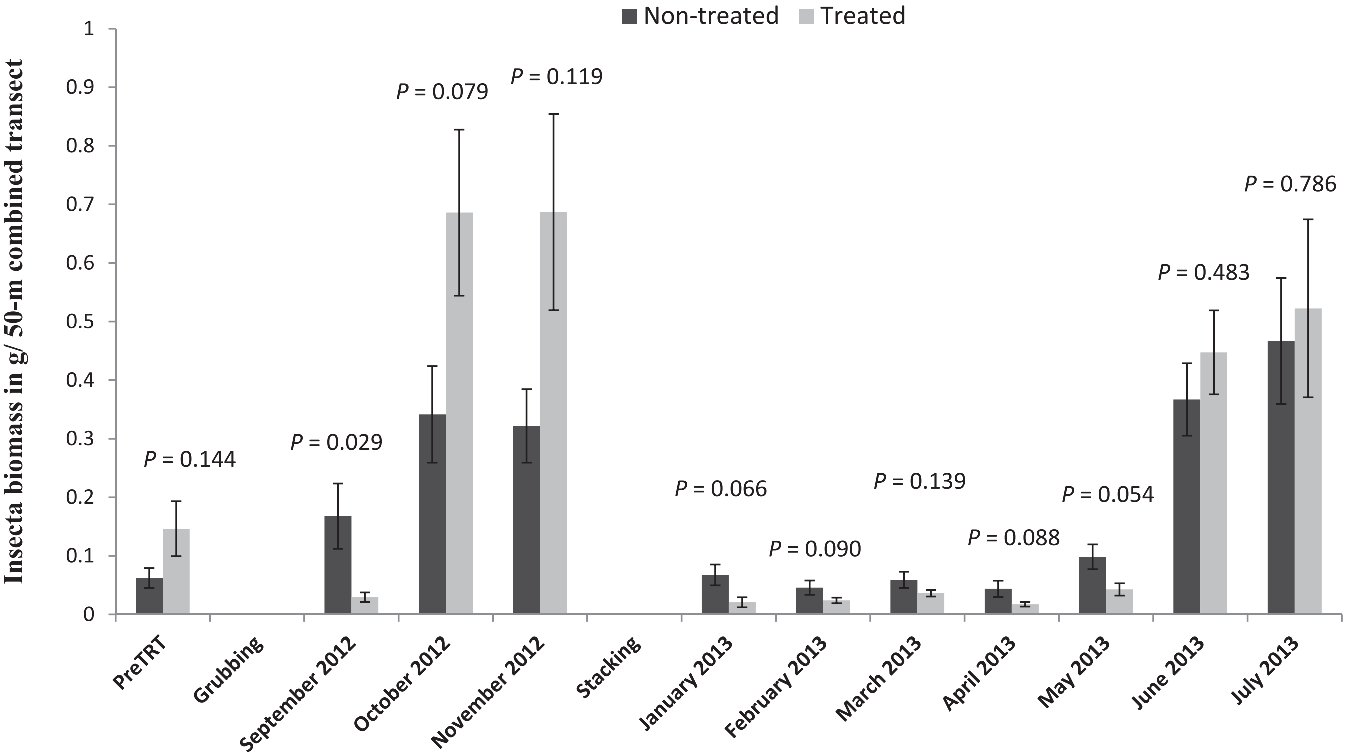

Fig. 7. Insecta biomass (Mean ± SE)/50-m combined transect (25-m sampled with a sweep net and 25-m sampled with a D-Vac). Treated represents grubbed and stacked sites and nontreated represents nontreated sites on the Santa Gertrudis Division of King Ranch, Inc. (Kleberg County, TX, USA). *P*-values obtained by analysis of variance tests of treatment effects within date. Treatment × date ($F = 3.002$), treatment within date effects: July 2012 ($F = 2.607$), September 2012 ($F = 6.36$), October 2012 ($F = 3.934$), November 2012 ($F = 2.867$), January 2013 ($F = 4.444$), February 2013 ($F = 3.548$), March 2013 ($F = 2.644$), April 2013 ($F = 3.789$), May 2013 ($F = 4.875$), June 2013 ($F = 0.538$), July 2013 ($F = 0.078$).

Grubbing and stacking can be used to alter habitat and food sources for bobwhite. However, we have little evidence that it changes the habitat drastically during drought conditions. Treatments were applied in strips, so thick brush cover is left adjacent to these open strips. The more open area is far easier to navigate for hunters and the visibility of bird dogs has been increased so treatments may allow hunters to access thicker brush areas that were more or less unhuntable, prior to treatment.

ACKNOWLEDGMENTS

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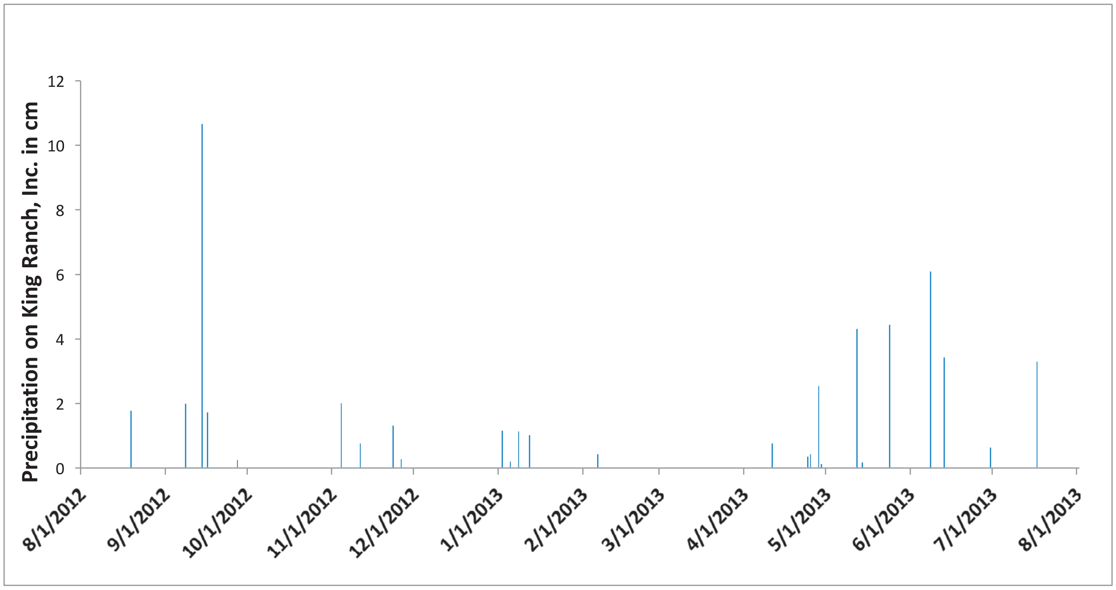

Appendix A. Precipitation data obtained from King Ranch, Inc., Kleberg County, Texas, USA. The blue bars represent daily precipitation totals in cm from 1 August 2012 to 1 August 2013 recorded at the Canelo Pens rain gauge (located between the treated and nontreated sites).

PREDICTING NORTHERN BOBWHITE HABITAT IN SEMIARID RANGELAND USING LANDSAT IMAGERY

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ABSTRACT

Multiple studies have attempted to model northern bobwhite (*Colinus virginianus*) distribution using classified remotely sensed imagery in combination with pattern recognition software. These models tend to be more accurate in humid subtropical regions. To identify bobwhite habitat in subhumid and semiarid rangeland, we performed our own classification on 4 LANDSAT scenes of Clay County, Texas, from July and December 2015. Stands of mature little bluestem (*Schizachyrium scoparium*) provide excellent bobwhite nesting cover and could be identified using LANDSAT imagery. Habitat was scored from 0 to 1.0 based on estimated range health, presence of little bluestem, and presence of brushy cover. We compared habitat score with the results of breeding season call counts from 2014 and 2015 and found significant correlation. When used in combination with other landscape data, this approach can provide a regional context to inform conservation and management decisions.

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Key words: call counts, *Colinus virginianus,* GIS, habitat, LANDSAT, modeling, northern bobwhite, populations, remote sensing, Texas

Northern bobwhite (*Colinus virginianus*) populations in the United States and Canada have declined >75% over the past 45 years and have been declining regionally for >100 years (Lewis 1863, Thorpe 1869, Judd 1905, Nice 1910, Errington and Hamerstrom 1936). The decline has been ascribed to many factors (Allen 1864, Nice 1910, Leopold 1937, Allen et al. 2004, Hernández et al. 2005) but research has generally implicated range-wide habitat loss, fragmentation, and degradation as the leading causes (Klimstra 1982; Brennan 1991, 1994; Williams et al. 2004; Hernández et al. 2012). Despite >75 years of habitat-driven research and management practices, northern bobwhite populations continue to decline (Hernández et al. 2012). Williams et al. (2004) suggested that this is because our current habitat management practices are implemented at the wrong spatial scale. Most bobwhite research on habitat to date has been done on a local (<25-km^2) scale (Kabat and Thompson 1963, Burger and Linduska 1967, Wiseman and Lewis 1981, Taylor et al. 1999a, Fies et al. 2002, Oakley et al. 2002, Riddle et al. 2008, Crosby et al. 2013) whereas harvest management is usually on a statewide scale (Williams et al. 2004). There is a need to transition from both local and statewide practices to more regional management (Peterson et al. 2002, Dimmick et al. 2002, Williams et al. 2004). One difficulty with regional management of bobwhite populations as proposed by Williams et al. (2004) is that quail managers do not know how large a bobwhite population is, or how large it must be to allow the population to persist for a set length of time. Estimates based on mathematical models range from 100 to 800 birds, depending on weather events and harvest (Guthery et al. 2000, DeMaso et al. 2011) but these estimates have not been tested. Quail managers need, also, to have a practical and reliable method to identify and prioritize bobwhite habitat on a regional level in order to determine the extent of the habitat loss and its implication for northern bobwhite populations. Our objective is to use freely available LANDSAT imagery to identify regions of northern bobwhite habitat and predict the distribution of bobwhite populations within the southern Great Plains region of Texas.

Scientists have attempted to generate models that relate bobwhite presence or abundance to local landscape cover using remotely sensed data for humid subtropical regions of the United States (Roseberry et al. 1994, Roseberry and Sudkamp 1998, Schairer et al. 1999, Peterson et al. 2002, Smith and Burger, Jr. 2004, Duren et al. 2011). Of these studies, only 2 performed their own landscape classification. Roseberry et al. (1994) performed a spectral classification on LANDSAT Thematic Mapper ($^{\mathrm{TM}}$) data and combined it with regions manually digitized from aerial photographs or mapped in the field. Smith and Burger, Jr. (2004) used LANDSAT Enhanced Thematic Mapper 7 data and Ikonos satellite 4-m-resolution imagery to divide their study area into 4 different land-cover categories, or classes. The other models used preclassified data such as US Geological

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Survey Land Use and Land Cover or the National Land Cover Database (Twedt et al. 2007), state land-cover databases (Roseberry and Sudkamp 1998), the Coastal Change Analysis Program (Duren et al. 2011), or the National Agricultural Statistics Service (Peterson et al. 2002), further aggregating the preclassified data into 5–9 broader classes. Although excellent for detecting trends in land use over time, these preclassified data are not particularly accurate at fine scales (Wickham et al. 2010, 2013). Even for level I classifications, such as distinguishing between urban, water, grassland and forest, National Land Cover Database accuracy averages approximately 85%. More specific classifications have <80% accuracy, with those separating grasslands or cropland from pasture far lower (Wickham et al. 2013). Another factor overlooked by most models is the varieties of habitat that are often lumped together under agriculture or grass. In their examination of Conservation Reserve Program effects on bobwhite habitat, Roseberry et al. (1994) did consider 5 different grass, range, or cropland classes; however, all of the other bobwhite habitat models used 1–3 classes. None looked at more than a single class of rangeland, such as distinguishing between native and nonnative (improved) pasture grasses.

This oversight is of particular importance to regions where most bobwhite habitat is located on rangeland because rangeland varies considerably in the quality of bobwhite habitat it provides based on the amount of woody cover, herbaceous cover, percentage of bare soil, grass height, and the relative diversity of grass and forb species (Rice et al. 1993, Kopp et al. 1998, Taylor et al. 1999a). When available, bobwhites tend to use mature stands of bunchgrass as nesting cover (Harshbarger and Simpson 1970, Taylor et al. 1999b), though other plants, such as prickly pear (*Opuntia* spp.), are also used (Hernández et al. 2003, Hernández and Peterson 2007). Posthatch, bobwhites require loafing cover for resting during the heat of the day (Stoddard 1931, Carroll et al. 2015b), such as brush and small trees (Johnson and Guthery 1988). The presence of brush can also be important for nest-site selection (Carroll et al. 2015a). Posthatch through maturity, bobwhites also require “brood cover” habitat consisting of shade, overhead protection from aerial predators, and food-producing forbs (Stoddard 1931, Handley 1931, Hurst 1972).

Little bluestem (*Schizachyrium scoparium*) is perhaps the most important plant in semiarid rangeland for northern bobwhites. In Texas and Oklahoma, mature little bluestem is by far the preferred bunchgrass for nesting cover (Lehmann 1984, Townsend et al. 2001). In some studies, bobwhites exhibited a >90% preference for little bluestem as a nesting site (Peoples et al. 1996, Hernández et al. 2003). Bobwhite are also associated with little bluestem stands outside of nesting season, preferring bluestem interspersed with shrubs or other woody cover (Johnson and Guthery 1988, Hernández and Peterson 2007, Richardson et al. 2008). Additionally, brood cover typically contains little bluestem (Wiseman and Lewis 1981, Hernández and Peterson 2007, Richardson et al. 2008), though bobwhites have a propensity for areas with more open ground along with taller vegetation to provide greater visual obstruction from above (Taylor et al. 1999b, Hernández and Peterson 2007). Little bluestem is a major focus of our study because of its near-exclusive use as nest sites for bobwhite in our study area and its strong association with other bobwhite habitat types.

Little bluestem is also expected to be quite detectible from satellite imagery. During the autumn and winter, little bluestem has a distinctive orange–bronze color (Kratsch and Hunter 2009, Davis 2011) that can improve the chance of distinguishing it from other grasses, particularly when viewing satellite imagery from >1 season (Guo et al. 2003). This means that locating ≥1 component of bobwhite habitat (i.e., nesting sites) based on the reflected color of vegetation may be easier in North Texas and western Oklahoma than in other parts of the bobwhite range where little bluestem is less common and other bunchgrasses are used for nesting cover.

There have been some attempts to categorize quality of rangeland as measured by grass height and percentage of bare ground (Guerschman et al. 2003, Röder et al. 2008) using LANDSAT or other satellite imagery. Reduced vegetation as produced by overgrazing increases surface albedo (Jackson et al. 1975), which can be detected both in the visible and infra-red spectrum (Michalek et al. 2001). Loafing cover types such as shrubs and other aerial cover are also identifiable in aggregate from satellite imagery (Boyd 1986, Afinowicz 2004), although we may not reliably be able to detect smaller scale brood cover. However, the limited range and movement of bobwhites (Terhune et al. 2006b, Brennan et al. 2014) would strongly imply that brood cover will be located near nesting and loafing cover. Based on this assumption, a bobwhite habitat model based on the presence–absence of little bluestem and other cover types that are detectable through satellite imagery is feasible for our study area.

The LANDSAT program is one of the most commonly used sources of remote sensing imagery because of its >40-year history and low cost data (Jensen 2005, USGS 2013). LANDSAT 8 scenes include 11 bands of data (USGS 2013), each formatted as a black and white raster image and covering a different portion of the electromagnetic spectrum (Table 1). These bands can be used to gather information about vegetation type and vegetation health, including rangeland quality (Lauver and Whistler 1993; Harvey and Hill 2001; Sims and Gamon 2002, 2003; Schmidt and Skidmore 2003) though the discriminatory power may be lower in arid regions (Okin et al. 2001). Using LANDSAT imagery, we hypothesize that we can predict the location of specific components of bobwhite habitat and, therefore, bobwhite populations in our study area.

STUDY AREA

The study area for this project was Clay County, located in the Central Great Plains ecoregion of North Texas (Griffith et al. 2004). Clay County (2,844 km^2) consisted of >56% pasture, crop- and rangeland (Homer et al. 2015, USGS 2015). Clay County also had >1,800

Table 1. LANDSAT 8 bands, wavelengths, and resolutions (USGS 2013) acquired 11 July 2015 and 18 December 2015 in Clay County, Texas, USA, from which were derived land-cover classes to evaluate habitat use by northern bobwhites. Wavelength is in μm, resolution in m. Before classification, band 8 was discarded and bands 10 and 11 were resampled to the same 30-m resolution as bands 1–7 and 9 (Xian and Crane 2005, Deng and Wu 2013).

Band	Wavelength	Resolution (m)
1	0.43–0.45	30
2	0.45–0.51	30
3	0.53–0.59	30
4	0.64–0.67	30
5	0.85–0.88	30
6	1.57–1.65	30
7	2.11–2.29	30
8	0.50–0.68	15
9	1.36–1.38	30
10	10.60–11.19	100
11	11.50–12.51	100

km of publicly accessible roads from which to collect data in addition to access granted from private ranches. The vegetation was primarily Mesquite–Lotebush vegetation with portions of Post Oak Parks, Mesquite Brushland, cropland, and Cottonwood–Hackberry Forest to the north, along the Red River (McMahan et al. 1984).

Climate in Clay County was characterized by hot summers and cool winters. Mean monthly low temperatures in Henrietta, the county seat, ranged from –2° C in January to 22° C in July. Mean monthly high temperatures ranged from 12° C in January to 36° C in August. Mean annual precipitation in Henrietta 1981–2010 was 83 cm with May, June, and October the wettest months (Arguez et al. 2011). Monthly precipitation amounts as measured at the nearest official National Weather Service recording station ranged from 0 cm for May 2014 to 43 cm for May 2015 (National Weather Service 2015, 2016).

METHODS

We established data collection points for recording quail breeding calls and habitat information along public and private roads across Clay County. We selected points based on the local landscape to avoid establishing points in areas that would prohibit hearing calls (i.e., behind trees or in low-lying areas). Bobwhite vocalizations can be heard up to 1 km away under ideal conditions (Rusk et al. 2007) with mean distances of 500–800 m as determined by field tests (Bennitt 1951). To minimize overlap, we placed points 1–2 km apart at a suitable location, usually the top of a hill or small rise, nearest to a 1.6-km straight-line distance from a previously established point. We recorded coordinates (latitude and longitude) of each point with a handheld Global Positioning System (GPS; Garmin, GPSMAP® 64st, Olathe, KS, USA).

To create a Clay County population index, field technicians recorded bobwhite breeding season calls at each point. The date of peak bobwhite calling activity can vary from year to year. Peaks typically occur between 1 June and 10 July (Bennitt 1951; Rosene 1957, 1969; Robel et al. 1969). We recorded calls from 16 May to 24 June 2014 and 19 May to 30 June 2015 because calling begins earlier in southern latitudes (Rosene 1969). All field technicians were trained by accompanying experienced observers in the field prior to the start of call counts. Each technician was assigned a region each day and provided with a pen, map, compass to determine cardinal directions, clip board with data recording sheets, hand-held GPS with the coordinates of each point, and Kestrel 3500 Weather Meter (Nielsen-Kellerman, Boothwyn, PA, USA). Beginning at sunrise, technicians recorded the approximate distance and direction of each male bobwhite heard for a 5-minute duration (Terhune et al. 2006a). Technicians were instructed to move >20 m from the vehicle before recording. Technicians recorded local weather conditions at each stop using the Pocket Weather Meter. Listening times in the third hour after sunrise give negligible undercounts for lower density sites (Hansen and Guthery 2001) and calling activity drops significantly after the third hour (Bennitt 1951); therefore, we limited data collection to a 3-hour period following sunrise. An increase in wind speed is significantly negatively correlated with the number of bobwhites audible (Bennitt 1951, Robel et al. 1969, Hansen and Guthery 2001) so technicians did not record if local winds exceeded 16 km/hour. Call counts were not conducted during rain (Hansen and Guthery 2001). A replicate survey of all points was logistically unfeasible but 80.9% (545/673) were visited two or more times. The number of male bobwhites recorded at each point was averaged before analysis.

For improved visualization, the call count data were interpolated (Valley et al. 2005), a transformation of point measurements into a 2-dimensional x–y raster surface with pixel "brightness" values representing the z-axis. In this case, we used the number of bobwhites recorded as the z-value. Converting the call count data to raster format has another advantage in that it is easier to make regional comparisons between different years. There are >15 methods for interpolation (Triebel 1995). The numbers of bobwhites heard per listening station can vary, so interpolation was performed by Kriging (Krige 1951), which is an interpolation method designed to accommodate multiple values for single points (Matheron 1963) to estimate a variable local mean (Saito et al. 2005). Kriging was performed in ArcMap 10.1 at the default resolution (~270 m on this map) using the nearest 6 points, based on bobwhite detection probability from Riddle et al. (2010) and Pellet and Schmidt's (2005) method to determine the number of site visits required to infer absence. The maximum radius was set at 6 km, the maximum seasonal distance travelled by bobwhites as reported by Fies et al. (2002).

To address habitat assessment for the model, we downloaded imagery acquired by LANDSAT 8 from 2 different seasons (11 Jul 2015 and 18 Dec 2015) from the US Geological Survey Earth Explorer website (http://earthexplorer.usgs.gov). Dates were determined by the

Table 2. Land-cover classes, subclasses, and relative habitat suitability scores for northern bobwhite habitat in Texas, USA (Jul and Dec 2015). Subclasses were scored based on division of bobwhite habitat requirements into nesting cover, shade (overhead cover), and food and range from 0 (poor) to 1.0 (excellent).

Class	Subclass	Value
Water	Water	0.0
	Silty water	0.0
	Flooded regions	0.25
Forest	Bottomland hardwood	0.375
	Other deciduous	0.5
	Mixed or Unclassified	0.5
	Scattered trees	0.5
Brush	Brush	0.5
Grasses	Cropland	0.25
	Rangeland, (<10 cm)	0.25
	Rangeland, with brush	0.375
	Rangeland, (10–20 cm)	0.375
	Rangeland, with brush	0.50
	Rangeland (>20 cm)	0.75
	Rangeland, with brush	0.875
Little bluestem	Bluestem	0.875
	Bluestem, with brush	1.0
No vegetation	Concrete or Urban	0.0
	Bare soil	0.125

availability of high summer images (brush assessment) and early winter images (locating stands of little bluestem) with 0% cloud cover. For analysis, we resampled the thermal infra-red bands to the same 30-m-resolution as bands 1–7 and 9 (Xian and Crane 2005, Deng and Wu 2013) using the nearest neighbor interpolation to retain original brightness values. To make the data easier to use, we combined individual raster layers into a single file for each season using the GeoTIFF format. Although the LANDSAT panchromatic layer can result in improved classification because of more precise positional location of features, the effect is greatest in urban environments (Sunar and Musaoglu 1998). Masek et al. (2001) found the difference in classified areas to be $\leq$3%. The panchromatic band was discarded and National Agriculture Imagery Program imagery (30 Jun 2014) with $\leq$1-m resolution was used to assist with classification and location. Because Clay County lies on a boundary between 2 horizontal LANDSAT rows, each season required 2 LANDSAT scenes to be combined: path 28, row 36 and path 28, row 37, and path 27 row 37. We combined 2 scenes for each date into one using the Mosaic to New Raster tool in ArcMap v. 10.1 (Environmental Systems Research Institute, Redlands, CA, USA) and the blend option so each pixel value in the overlapping region was determined by the image with the viewing angle closest to 90°. We then cropped the new rasters to the area of interest to create 2 single-date 30-m-resolution coverages of Clay County with a 1-km buffer.

We performed an unsupervised ISO classification on each GeoTIFF in ArcMap. We grouped pixels into 100 clusters mathematically based on their reflective properties (Jensen 2005). We then assigned clusters to land-cover categories by analysis of National Agriculture Imagery Program aerial photography and Google Earth v. 7.1.5.1557 (Google, Menlo Park, CA, USA). To evaluate the classification, we selected 200 pixels (100 for little bluestem due to scarcity in accessible regions) from each of the major classes at random for those that could be assessed from high-resolution aerial imagery (water, forest, brush, bare ground) or at random within accessible areas for classes that had to be evaluated *in situ* (grasses, bluestem). We exported these into a shapefile and then converted them into Keyhole Markup Language (KML) and GPS Exchange Format (GPX) files using DNR GPS v. 6.1.0.6 (Minnesota Department of Natural Resources, St. Paul, MN, USA). We assessed accuracy through Google Earth imagery and by *in situ* evaluation by automobile or all-terrain vehicle using a handheld GPS for navigation. Local heterogeneity made classification more problematic. Pixels evaluated by aerial imagery were considered correctly classified if >50% of the pixel in question matched the predicted land cover. The same threshold was used for pixels evaluated *in situ*, excepting those divided by fences or ranch roads. For divided pixels, the threshold was 33%.

In order to score each land-cover type based on its utility for bobwhite, we simplified the bobwhite habitat requirements into nesting cover, shade (overhead cover), and food. We weighted little bluestem (nesting cover) at 0.5 because bobwhites almost exclusively use this plant for nesting in the southern Great Plains (Peoples et al. 1996, Hernández et al. 2003) and it was relatively rare, occurring in detectable amounts in <8% of our study area. We weighted shade and food at 0.25 each. In theory, any plant taller than a bobwhite can provide overhead cover and the bobwhite diet is so varied in plants and insects (Judd 1905, Nice 1910, Brennan and Hurst 1995, Butler et al. 2012) that most land-cover types provide one or both of those requirements for at least part of the year. We gave each land-cover type a score based on which requirements were met and whether those requirements were provided for part of the year (×0.5) or for the entire year (×1.0). For example, cropland can provide both shade and food but LANDSAT imagery shows that cropland is bare or near bare in December during planting season, and in July following a harvest so neither food nor shade is available year round. This applies both to wheat and to cool-season grasses that make up the vast majority of crops grown in Clay County, so cropland was scored as $[0.25(0.5) + 0.25(0.5)]$, or 0.25 total. Bare soil provides no shade but can provide food at least part of the year (Baker and Guthery 1990) because seeds from nearby plants are exposed. Where this was applicable, we scored bare ground as $0.25(0.5) = 0.125$. Individual habitat-type scores ranged from 0.0 to 1.0 (Table 2).

Once scored, we created 2 new rasters—one for July and one for December—using the habitat suitability score as the pixel values through the ArcMap Lookup tool. To combine the 2 rasters into a single value, we multiplied the value of each pixel in one raster by the value in the corresponding pixel in the other raster to create a new raster of estimated year-round habitat suitability (Fig. 1). We chose multiplication to increase the variance while

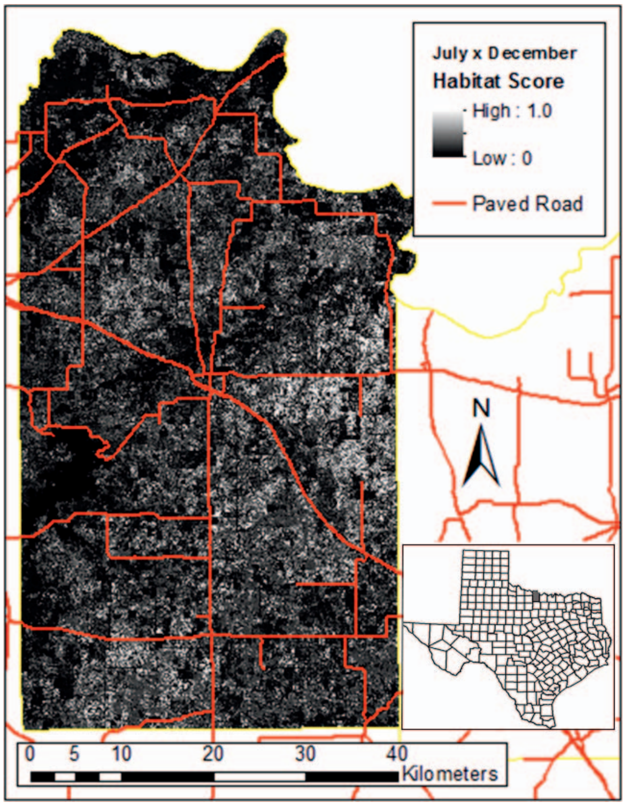

Fig. 1. Clay County habitat scores based on land-cover classes derived from 30-m resolution LANDSAT 8 imagery acquired 11 July 2015 and 18 December 2015. Value is based on utility for northern bobwhite where nesting cover = 0.5, year-round brood–loafing–aerial cover = 0.25, and year-round food availability = 0.25. Inset shows study area location within Texas, USA.

maintaining habitat values ≤ 1.0. The habitat suitability map had a 30-m-pixel resolution derived from 30-m-resolution raster data while the call count maps had an approximately 270-m-pixel resolution derived from points 1–2 km apart. The habitat suitability map also needed to be smoothed to moderate the negative habitat bias of gravel or bare soil and mowed right-of-ways associated with the roads where most call-count data were collected. Terhune et al. (2006b) reported a maximum mean daily movement of 298 m for resident bobwhites so we gave each cell in the habitat map the mean score of a 300-m-radius circle surrounding the cell using the Focal Statistics tool. We assumed this to represent the aggregate quality of habitat any particular male may have traveled through that day. We then resampled the habitat suitability map to the same pixel resolution as the call count raster. We extracted the habitat value at each point to give a series of values to statistically compare with the bird count data taken at the same points. Like the aforementioned call count data, the habitat values at the points were then interpolated using Kriging through the nearest 6 points. Performing the same operation used for the call count data provided an easily interpreted conservation tool for visualizing the estimated quality of bobwhite habitat across multiple properties.

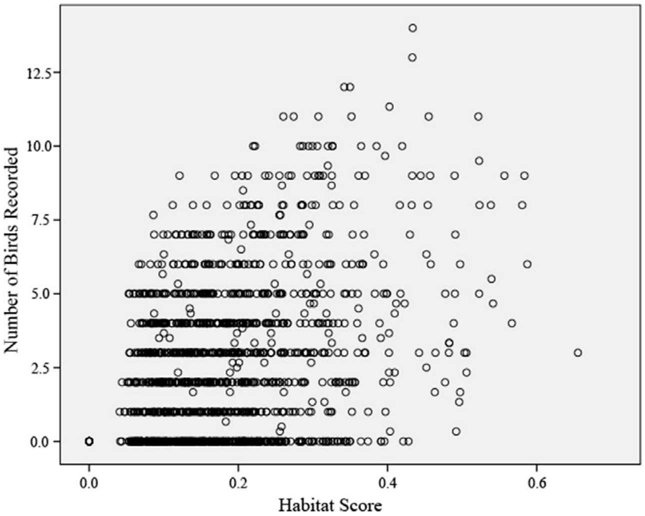

Fig. 2. Raw number of northern bobwhites recorded at each data collection point (DCP) in Clay County, Texas, USA (Jul and Dec 2015), as a function of mean estimated habitat score based on LANDSAT 8 imagery.

RESULTS

Bobwhite calls were recorded at 545 locations in 2014. An additional 128 points were added in 2015 for a total of 673. The mean number of bobwhite calls per location was correlated (Spearman's rank correlation coeff., $n = 673$, $\bar{x} = 2.88$, $\rho = 0.31$, $P < 0.0001$) with the estimated (smoothed) habitat value (Fig. 2), indicating that the location of bobwhite populations can be predicted using LANDSAT imagery. For visual comparison, the map generated using only the estimated habitat data from the same points as where the call count data were recorded (Fig. 3B) looks remarkably like the map generated from the call count data (Fig. 3A).

Accuracy for the land-cover classification ranged from 100% for water to 66% for brush (Table 3). The accuracy for little bluestem was 73%. Interestingly, 24 of the 27 false positives for little bluestem were broomweed (*Amphiachyris* spp.), which is not nesting cover but still a potentially useful brood cover plant (Chenault 1940, Lehmann and Ward 1941). Subcategory classification within the grasses was less successful. Rangeland was distinguished correctly from cropland 85% of the time but only 68% of the rangeland classes were correctly identified with differences in plant height accounting for most of the error. Surface completely lacking plant cover could be identified correctly 93.5% of the time the classification process could not reliably distinguish between concrete and bare soil or rock.

DISCUSSION

Although the model generated from the 2015 data significantly correlated with the number of male bobwhites heard, the overall correlation was relatively low ($\rho = 0.31$). We demonstrated that little bluestem, as detected from satellite imagery, could predict bobwhite presence when combined with additional land-cover data in a

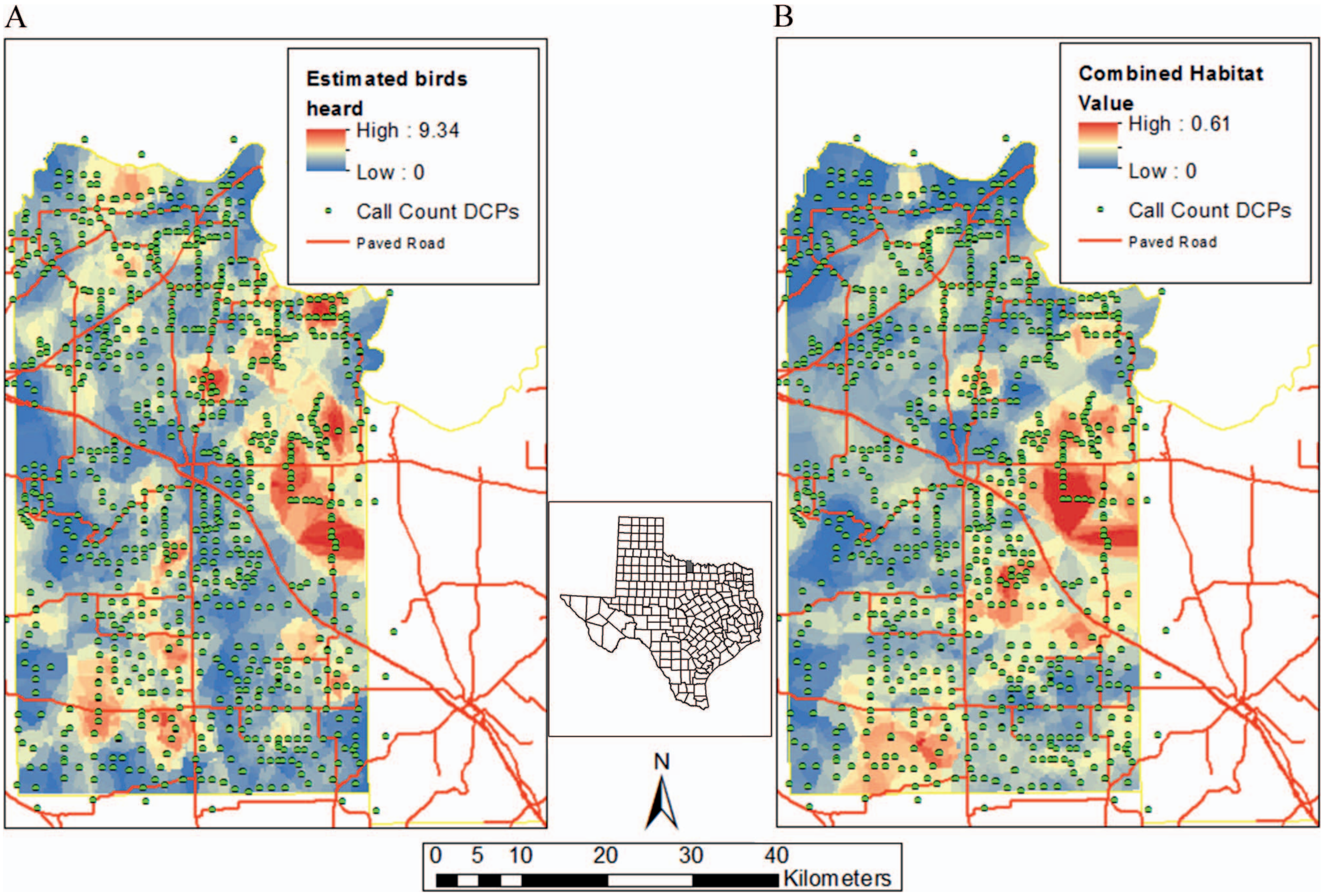

Fig. 3. Estimate of surface values interpolated via Kriging from 1,218 call counts at 673 data collection points during July and December 2015. (A) Interpolation based on number of male northern bobwhites heard at each data collection point. (B) Mean estimated habitat values within a 300 m of point based on classification of LANDSAT 8 imagery. Inset shows study area location within Texas, USA.

simplified additive model. Future model performance may be improved by considering additional factors. For example, bobwhite density may be inversely correlated with mean land-parcel size (Patten et al. 2005) or oil well density (Doherty et al. 2008, Carpenter et al. 2010). Habitat models vary greatly in predictive ability and are typically limited to a single region (Fielding and Haworth 1995). An increase in accuracy locally may decrease the applicability of the model to other regions, a factor that must be considered as we refine and test this model in additional locations within the Central Great Plains ecoregion of North Texas

One source of error for our current model was classification inaccuracies due to factors such as grass height. Little bluestem can be detected using freely available LANDSAT imagery but quality of rangeland is more difficult to distinguish, at least with the techniques described here. Error rates were higher in the landscape categories most likely to contain bobwhite (rangeland and rangeland with brush), particularly with regards to grass height. There may also be limitations on the utility of the image data for performing detailed, large-scale analyses. For example, brush was more reliably detectable in the eastern portion of the study area than in the western portion, suggesting that subtle differences in satellite viewing angle influence reflected color. Future classifications may be made using data provided by The ESA's Sentinel program, which had a higher orbital altitude and narrower sensor footprint than LANDSAT (Malenovský et al. 2012, Drusch et al. 2012).

The weather in 2015 presented another confounding factor. Spring and summer rains in 2015 caused widespread flooding throughout Clay County after 4 years of extreme drought (Wang et al. 2015). Some data points were inaccessible for days or weeks. Above-average precipitation continued into December and several misclassified pixels were directly attributable to higher than normal soil moisture. In an extreme example, 4 test pixels in low-lying portions of recently planted cropland were classified as forest.

The limitations of single-observer roadside counts are well-documented (Anderson 2001, Rosenstock et al. 2002, Royle and Nichols 2003, Applegate et al. 2011). The number of birds heard at each point represent an unknown fraction of the true number of birds within hearing range. However, single-observer counts are often the most efficient way to survey a large area, despite the variance. In order to determine the true number of birds at

Table 3. Land-cover classification accuracy for northern bobwhite habitat in Texas, USA (Jul and Dec 2015). Main class accuracy is a percentage. For subclasses, ratios are shown. Test pixels were selected from each class either at random (water, forest, brush, bare ground) or at random within 30 m of roads or on properties that allowed access (grasses, bluestem). Accuracy for water, brush, and forest was assessed using Google Earth. Accuracy for grasses was assessed by travel to the test pixel.

Class	Accuracy (%)	Subclass	Accuracy
Water	100	Water	178/178
		Silty water	18/18
		Flooded regions	3/3
Forest	93	Bottomland hardwood	74/79
		Other deciduous	22/29
		Mixed or Unclassified	66/86
		Scattered trees	4/6
Brush	66	Brush	132/200
Grasses	87.5	Cropland	34/40
		Rangeland, (<10 cm)	19/28
		Rangeland, with brush	4/8
		Rangeland, (10–20 cm)	20/33
		Rangeland, with brush	6/9
		Rangeland (>20 cm)	11/17
		Rangeland, with brush	3/5
Little Bluestem	73	Bluestem	52/76
		Bluestem, with brush	17/24
No cover	93.5	Concrete or Urban	105/138
		Bare soil	35/62

each point, one must know the probability of detecting an individual bird (Nichols et al. 2000). Going forward, point counts will make use of multiple observer (Nichols et al. 2000, Alldredge et al. 2006) and removal model (Farnsworth et al. 2002) techniques to estimate the probability of detection.

It should also be noted that this is a landscape-level evaluation. It can identify regions with probable bobwhite populations, or at least those with potential, but it may be of little use on a finer scale within those areas. Although Duren et al. (2011) found that landscape-level factors had a greater influence on distribution than local variables, there is still considerable variation in local distribution. The factors influencing local distribution may not be known or, if known, may not be detectable from satellite imagery.

MANAGEMENT IMPLICATIONS

The National Bobwhite Technical Committee (2011) recommended conservation policies be considered at ecoregion levels of 25,000–300,000 km^2. As management focus moves from a local to a regional scale, there is an increased need for regional data on habitat quality and bobwhite populations as well as data that can be used across multiple scales. This analysis is on a smaller scale, $<$3,000 km^2; however, the techniques used in this study can be applied on an ecoregion scale, with the potential to identify focal areas across all of the Cross Timbers region in Texas and much of the Central Great Plains to assist with prioritizing use of scarce resources in identifying these focal areas. It can also help with locating populations susceptible to local extirpation as well as regions of marginal habitat to consider for rehabilitation (Williams et al. 2004).

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THE ROLE OF JOINT VENTURES IN NORTHERN BOBWHITE CONSERVATION

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Abstract

Partnerships are crucial part of northern bobwhite (*Colinus virginianus*) conservation. A key principle is that no single entity can effectively address the complex landscape-level conservation issues to sustain populations and their supporting habitats in perpetuity. Joint Ventures (JVs) use a partnership based approach to deliver specific bird population and habitat objectives within their geography. Currently, 7 of the 12 JVs that occur in the North American bobwhite range have bobwhites listed as a priority species. This presentation will cover various topics including: 1) the history of JVs in North America; 2) an overview of the variety of models used in these partnerships to achieve bird conservation; 3) strategic habitat conservation framework applied to bobwhite conservation within the Gulf Coast Joint Venture; and 4) a discussion of bobwhite conservation products developed by some of the JVs that reside within the bobwhite range in North America.

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Key words: *Colinus virginianus*, conservation, habitat, northern bobwhite, population

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LONG-TERM POPULATION STABILITY IN THE GREATER RED HILLS REGION AMIDST RANGE-WIDE DECLINES: A CASE FOR INTEGRATED MANAGEMENT

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ABSTRACT

All natural habitats possess inherent conservation value, including the presence of rare or endemic species, provision of ecosystem services, historic landmarks, or resources harvested. Large-scale loss of natural habitats and deterioration of fire-mediated habitats has caused precipitous declines of native fauna and flora in the southeastern US. The role of private landholdings in wildlife and conservation is often underestimated, and consumptive use of wildlife is commonly viewed as counterproductive to sustainability. However, in the Greater Red Hills region (GRH) of north Florida and south Georgia, intentional management for northern bobwhite (*Colinus virginianus*) on private lands has not only created "huntable" and sustainable bobwhite populations but also enhances overall conservation value among working landscapes – the overall estimated economic value of the GRHs properties is $272 million. Despite range-wide population declines in bobwhite abundance, proper application of frequent fire combined with sound forest management has yielded bobwhite densities of 4—8 bobwhites/ha. This intentional and intensive management has facilitated preservation of ecosystem integrity and profited numerous declining, threatened or endangered species. Thus private lands, which encompass two-thirds of the US, are critically important for maintaining biotic diversity and wildlife populations. Many conservation action plans (e.g., NBCI) underscore the importance of public lands, but few have quantified the conservation value of private lands intentionally managed for bobwhites. Yet, pressures are mounting for many private landowners to balance costs and benefits of management, and more effectively operate with fewer dollars. In many cases, lands not economically competitive for wildlife may shift toward agricultural, industrial, or residential uses in the future, diminishing the natural conservation value of these lands. Incentivizing private lands conservation (i.e., providing dollars, tax breaks) and strategically leveraging these landscapes as conservation centers may improve stability of bobwhites and other species in these regions, and expedite population expansion to surrounding areas.

Citation: Terhune II, T. M., D. C. Sisson, W. E. Palmer, and S. D. Wellendorf. 2017. Long-term population stability in the greater Red Hills region amidst range-wide declines: a case for integrated management. National Quail Symposium Proceedings 8:118.

Key words: Biodiversity, *Colinus virginianus*, conservation, Greater Red Hills, private land, northern bobwhite, value, working lands

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AN EVALUATION OF NORTHERN BOBWHITE CONSERVATION RESEARCH: A CALL FOR LARGE-SCALE STUDIES

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) populations have declined throughout the species' range since the 1960s. Habitat loss and degradation are thought to have largely contributed to this decline by reducing the amount of space and resources required to sustain viable quail populations. Previous studies have attempted to address this issue by focusing on ranch-level management of bobwhites instead of on the effectiveness of large-scale techniques. Here, we review current and historical studies that have facilitated the implementation of management techniques on multiple scales. In doing so, we will also reveal the shortcomings of such studies by highlighting their narrowed focus on small-scale management and research, and reiterate the need for large-scale studies.

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Key words: *Colinus virginianus,* conservation, habitat evaluation, northern bobwhite, population ecology, research practices, scale

The decline of northern bobwhites (*Colinus virginianus*) has been apparent for decades, with populations across their range currently deteriorating at a rate of >4.0%/annum (Sauer et al. 2014). This decline continues despite efforts to reverse the trend, indicating that predominate management strategies are either ineffective or lacking in some critical aspect. In the past, much of the effort in bobwhite management has been focused on a ranch or regional level, with little focus on large or landscape-level management (Brennan 1991, Williams et al. 2004*a*, Hernandez et al. 2013). Though many difficulties are associated with large-scale studies and implementing broad-scale management plans (Clark et al. 2015), there is increasing evidence that adopting a broad-scale management plan will be essential to the conservation of both bobwhites and other species associated with bobwhite habitat (Brennan and Kuvlesky 2005). The past 2 decades have seen the rise of large-scale management strategies for bobwhites; however conservation research trends may be slow to reflect these large-scale goals. A potential disconnect between research and management practices presents a challenge to conservation because small-scale research findings may not translate to the scale at which management is carried out.

In this review, we evaluate the relationship between bobwhite conservation management and research practices. We first examine the benefits and shortcomings of current and historical management and research. Second, we discuss changes in bobwhite research from the past 2 decades. Finally, we discuss 2 fundamental research questions that have yet to be answered and provide specific suggestions to improve research in both areas.

CHANGING PERSPECTIVES ON BOBWHITE MANAGEMENT

Northern bobwhites have historically been a popular game bird; and though the number of bobwhite hunters has decreased in tandem with the species' decreasing abundance, interest in conserving this species for sustainable harvest has persisted (Burger 2002, Williams et al. 2004*a,* Johnson et al. 2012). This popularity has both helped and hindered its conservation. Although hunter interest has aided in raising funds and awareness to protect bobwhites, this interest has ultimately abetted the precipitation of a culture and management style that was not designed to be primarily beneficial for large bobwhite populations. Rather, early management practices were meant to provide the greatest benefit to hunters and landowners by increasing quail abundance at minimum expense at a local level (Leopold 1933, Lehmann 1937, Johnson 1948, Williams et al. 2004*a*). This narrow interest led to the adoption of a symptomatic approach to quail management, whereby factors with potential negative impact on bobwhite populations were treated at a local level rather than addressed at a broad scale (Williams et al. 2004*a*). This symptomatic approach has included management measures such as food plots, predator control, and restrictions on bag limits (Guthery 1997). Although these approaches have the possibility of reaping beneficial impact on a local scale, they are

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impractical and have not been shown to affect broad-scale decline (Brennan 1991). Other issues addressed, such as red imported fire ants (Brennan 1993, Allen et al. 1995, Giuliano et al. 1996), helminthic parasites (Reed et al. 1981, Dunham et al. 2014), and mammalian generalist predators (Cox et al. 2004), as well as assessment of environmental factors such as precipitation (Hernandez et al. 2005) and thermal stress (Guthery et al. 1997, 2005; Hernandez et al. 2002*a*; Reyna and Burggren 2012), may have an impact on a broad scale but have mostly been studied at a local level.

Of the proposed causes for decline, the state of bobwhite habitat is now recognized as perhaps the most influential factor. Habitat management has always been a part of bobwhite management as the proper management of forest, prairie, and scrubland is paramount to sustaining and increasing quail abundance where quail are already present (Stoddard 1931, Brennan 1991). The importance of habitat has made it increasingly apparent that all of the aforementioned factors of decline are still yet symptoms of a larger problem—habitat degradation and fragmentation on a national scale. An estimated 80% of grass and shrub-land habitat has been lost in North America since the mid-19th century (Brennan and Kuvlesky 2005). Though quantifiable evidence of the bobwhite decline exists only as far back as the Breeding Bird Survey—approximately 60 years—this loss of habitat precedes estimates of the beginning of the bobwhite decline, circa 1875 (Peterson et al. 2002). Habitat loss is chiefly attributed to large, national-scale issues such as monoculture agriculture (Exum et al. 1982, DeMaso and Dillard 2007, Peterson 2007), afforestation (Brennan and Kuvlesky 2005), pesticide use (Brennan 1991), and urban or suburban development (Veech 2006); better said, human impact is likely the largest contributor to the bobwhite decline. This has caused conservationists to recognize 2 crucial concepts: 1) effective wildlife management is less about managing wildlife and more about managing people (Leopold 1933) as we are essentially battling ourselves to restore this species; and (2) a large-scale problem such as habitat loss warrants a large-scale response. In this way, previous small-scale management techniques and research have fallen short—their scope has been too narrow.

For the past 2 decades, bobwhite conservation has undergone a refocusing of scope; considerable effort has been made to manage bobwhites on a broad scale through programs such as the National Bobwhite Conservation Initiative, the North Texas Quail Corridor, and North Carolina's Cooperative Upland Habitat Restoration and Enhancement program, among others. These programs coordinate with local entities to manage vast quantities of land for bobwhites, and emphasize landscape-scale management (McKenzie et al. 2015). Although these efforts are laudable, it is not clear if the current scale of bobwhite conservation research reflects management scale, or if small-scale results can be generalized to management scale.

TWO DECADES OF BOBWHITE RESEARCH

To ascertain the prevalence of landscape-scale research, we conducted a scoping literature survey using the databases Wiley Online (John Wiley and Sons, Inc., Hoboken, NJ, USA) and Google Scholar (Google Inc., Mountain View, CA, USA). We also surveyed journal and symposia literature published in the past 2 decades of the National Quail Symposia (IV–VII). We limited our search to fieldwork and habitat or population studies of northern bobwhite quail published between 1996 and 2015, for which study area was described and size given or region described, if conducted on the regional level. We included studies in the National Quail Symposia for which only abstracts were available only if study area size was given in the abstract. We included studies that examined predation, survival, nest success, management practices and habitat manipulation, measures of abundance or density, migration or dispersal, modeling, and other features of population dynamics. We converted all study area sizes into hectares (ha) for analysis, unless only a region was described.

We chose to categorize studies into 3 rankings: ranch-level, landscape-level, and region-level. Choosing how to categorize studies based on study area size presented a challenge in that no formal definitions were found for these rankings. Ranch-level has been described as $\leq$2,000 ha (Sands et al. 2012*b*); however, this approximation appears rather conservative (Perez et al. 2002). Landscape-level has been described as areas encompassing approximately 1,000,000 ha (Sands et al. 2012*b*) but consistent measures have not been seen in the literature. Region is generally designated by ecoregion or as an area encompassing several landscapes. We chose to analyze the data using a slightly less conservative definition of ranch-level; we defined ranch-level as $\leq$5,000 ha, and landscape-level as $>$5,000 ha and $\leq$1,000,000 ha. Region was defined as an area greater than landscape-level ($>$1,000,000 ha). Many publications used more than one study area, so we chose to analyze the data by only looking at the largest study area listed. As a result of our broad definition of landscape-level and the fact that we omitted several articles at the ranch-level because they did not provide a study area size (e.g., Henke 2002), we assert that ranch-level studies are likely underrepresented in this analysis.

This scoping survey yielded 139 publications (Table 1). In our initial analysis, we divided studies into 2 time frames, each spanning approximately 1 decade. We then calculated the percentage of literature that each scale-rank made up, for each decade respectively. For the years 1996–2005, ranch-level studies made up 64.5%, landscape-level studies made up 22.6%, and region-level studies made up 12.9%. For the years 2006–2015, ranch-level studies made up 59.7%, landscape-level studies made up 31.2%, and region-level studies made up 9.1%. We conducted a second analysis wherein we pooled studies from both decades. For the combined years 1996–2015, ranch-level studies made up 61.9%, landscape-level studies made up 27.3%, and region-level studies made up 10.8%.

The call-to-action for large-scale bobwhite management was initiated a little more than 2 decades ago (e.g., Brennan 1991); therefore, we expected to see an increase in the number of landscape-scale studies from one decade to the next and this was true overall. From 2006 to 2015, studies performed at the landscape level made up 8.6% more of the literature than in the previous decade. However, during 2006–2015, ranch-level studies still accounted for 28.6% more of the literature than landscape-level. Furthermore, when considering literature in both decades combined, ranch-level studies made up 61.9% of the literature alone. We reiterate that ranch-level studies are likely underrepresented.

From the results of this scoping review, we observe that bobwhite conservation research is still being performed predominately at ranch-level. Although we contend that not all research should be performed at a landscape-level, we do stress that small-scale studies may not yield results that are generalizable or able to direct broad-scale management. It is important that scientists invested in bobwhite conservation expand their inquiries to the landscape-scale at which the previously listed conservation initiatives take place.

FUNDAMENTAL RESEARCH CONCERNS RELATED TO SCALE

Based on our literature review, we believe there are presently 2 fundamental concerns that have yet to be answered by current scientific pursuits. The first is how much space a viable population requires; and the second is what ecological processes affect the persistence of local populations and how those processes are affected by landscape features. Here, we exemplify the importance of these concerns and how research has potentially been unsuccessful in addressing them.

Habitat and Space

The first fundamental concern of bobwhite research is to determine how much space a viable population needs. Guthery (1999) postulated that quail abundance is density-dependent, primarily restricted by the amount of viable habitat in a particular space and time (Guthery 1999, Lusk et al. 2002). Recent research has led further credence to the importance of understanding and incorporating density-dependence into population models (DeMaso et al. 2013). Considering both bird density and space requirements, several models have been developed to estimate the spatial requirements of a viable population. Guthery et al. (2000) suggested 800 bobwhites would be stable in approximately 650 ha; Twedt et al. (2007) suggested a sustainable population of >400 birds was possible at 5,000 ha; and Sands et al. (2012*b*) suggested that a stable population may need anywhere from 800 to 9,600 ha. Whether or not such stable populations actually exist in the tested conditions is not clear, generating concern regarding usable space and using current bobwhite research to make management decisions—stable and viable populations of quail could potentially be larger than what pasture-scale research takes into account. Studies of declining populations of bobwhites have concluded that there is a need to increase the quantity of breeding habitat for quail, though whether or how far breeding habitat should be increased beyond the scope of ranch-level management is unclear (Collins et al. 2009). Crosby et al. (2013) demonstrated the unsuitability of pasture-scale management via habitat restoration through the Quail Habitat Restoration Initiative. The study examined 29 areas over a period of 3 years to determine whether habitat restoration projects by the initiative had a positive impact on bobwhite abundance. The study concluded that no positive impact could be observed and postulated that this lack of impact could be explained by the fact that bobwhite population ecology operates on multiple scales, and that pasture-scale management and study would not necessarily take all scales or associated processes into consideration (Crosby et al. 2013). Furthermore, Williams et al. (2003*a*) showed that density-dependent abundance in bobwhites varies within their geographical range; variation was highest in the periphery of their range and the authors postulated that this was likely due to environmental factors affecting habitat quality. Terhune et al. (2010) have also suggested that habitat of poorer quality may need to be larger in area to accommodate a stable population of bobwhites, though to what degree habitat quality affects increased spatial needs has not been elucidated. Therefore, the spatial needs of stable and viable populations could potentially be greater than study areas on which research is performed and from which management decisions are made.

Improvements to habitat study and management.—Characterizing habitat has been a large part of bobwhite management, though the majority of attempts to characterize habitat occur at a pasture-scale (Peterson et al. 2002). To better implement large-scale management, further research should be aimed at characterizing habitat at a landscape scale. Although habitat quality may seem to be the most important feature at a local scale, the importance of habitat patch size, configuration, type, and connectivity may be more apparent at the landscape level (Riitters et al. 1997, Duren et al. 2011). For bobwhite habitat, efforts have been made using tools such as GPS and LANDSAT imagery (Roseberry and David 1994, Roseberry and Sudkamp 1998, Schairer et al. 1999) natural and agricultural resource databases (Peterson et al. 2002, Veech 2006), models (Baker 1996), and aerial photography (Exum et al. 1982, Guthery et al. 2001, Weber et al. 2002), but methods should be further refined. Habitat modeling at multiple scales, such as that performed by Duren et al. (2011), may provide much-needed insights to different habitat variables, which can be used to guide management of a particular landscape.

Research findings indicate that restoration and proper management of large, contiguous tracts or patches of habitat should continue to be the goal of bobwhite conservation (Brennan 1991, Hernandez et al. 2013). Although current large-scale restoration and management

Table 1. Referenced articles published between 1996 and 2015 that we examined while evaluating the relationship between northern bobwhite conservation management and research practices, categorized according to scale-rank, with largest study area size listed. Multiple study areas in a single reference were treated as separate unless they were specifically described to be continuous, in which case study areas were combined.

Reference	Study area
Ranch	
Arredondo et al. 2007	1,966 ha
Brennan et al. 1997*a*	1,500 ha
Brennan et al. 1997*b*	1,500 ha
Brooke et al. 2015	3,330 ha
Crosby et al. 2013	192 ha
DeMaso et al. 2002	283 ha
DeMaso et al. 2011	1,966 ha
DeMaso et al. 2013	1,966 ha
DeMaso et al. 2014	1,966 ha
Dietz et al. 2006	607 ha
Doerr and Silvy 2002	260 ha
Guthery et al. 2001	200 ha
Guthery et al. 2004	796 ha
Guthery et al. 2005	796 ha
Haines et al. 2004	1,563 ha
Haines et al. 2006	1,563 ha
Harveson et al. 1997	48 ha
Hernandez et al. 2005	2,000 ha
Hernandez et al. 2006	2,000 ha
Hiller and Guthery 2005	802 ha
Hiller et al. 2007	796 ha
Holt et al. 2006	2,300 ha
Holt et al. 2012	2,300 ha
Janke and Gates 2012*a*	1,200 ha
Janke and Gates 2012*b*	1,200 ha
Janke et al. 2013	1,200 ha
Jones and Chamberlain 2004	700 ha
Jones et al. 2010	66 ha
Kuvlesky et al. 2002	1,093 ha
Liberati and Gates 2012	1,200 ha
Liu et al. 1997	563 ha
Liu et al. 2002	563 ha
Lusk et al. 2006*a*	796 ha
Madison et al. 1997	5 ha
Manley et al. 1997	2,900 ha
Martin et al. 2006	2,368 ha
Miller et al. 2012	1,570 ha
Nedbal et al. 1997	610 ha
Oakley et al. 2002	3,900 ha
Osborne et al. 2011	10.8 ha
Palmer and Wellendorf 2007	1,568 ha
Palmer et al. 2005	250 ha
Palmer et al. 2002	445 ha
Palmer et al. 2012	1,568 ha
Parsons et al. 1997*a*	563 ha
Parsons et al. 1997*b*	563 ha
Peters et al. 2015	3,330 ha
Piispanen and Riddle 2012	1,619 ha
Potter et al. 2011	2,360 ha
Puckett et al. 1997	640 ha
Rader et al. 2007*a*	2,000 ha
Ransom and Schulz 2007	499 ha
Rollins and Koennecke 2012	1,900 ha
Rusk et al. 2007	1,200 ha
Sands et al. 2012*a*	750 ha
Sands et al. 2012*c*	1,900 ha
Seckinger et al. 2006	2,217 ha
Sisson et al. 1997*a*	380 ha
Sisson et al. 1997*b*	316 ha
Sisson et al. 2002*a*	3,734 ha
Sisson et al. 2002*b*	324 ha
Smith and Burger 2006	3,172 ha
Staller et al. 2002	1,568 ha
Staller et al. 2005	1,568 ha
Suchy and Munkel 1997	793 ha
Tanner et al. 2012	3,300 ha
Taylor and Burger 1997	320 ha
Taylor et al. 1997*a*	320 ha
Taylor et al. 1997*b*	2,850 ha
Taylor et al. 1999	2,850 ha
Terhune et al. 2006*b*	3,734 ha
Terhune et al. 2007	304 ha
Terhune et al. 2010	1,092 ha
Townsend et al. 1999	284 ha
Trewella et al. 2012	800 ha
Unger et al. 2012	3,300 ha
Unger et al. 2015	3,300 ha
Villarreal et al. 2012	1,902 ha
Wellendorf and Palmer 2006	1,568 ha
West et al. 2012	515 ha
White et al. 2005	3,898 ha
Whitelaw et al. 2006	1,568 ha
Williams et al. 2000	2,849 ha
Williams et al. 2003*b*	259 ha
Williams et al. 2004*b*	259 ha
Williamson et al. 2002	4,048 ha
Landscape	
Berkman et al. 2013*a*	757,300 ha[a]
Berkman et al. 2013*b*	757,300 ha[a]
Blank 2012	340,065 ha[a]
Buckley et al. 2015	5,665 ha
Collins et al. 2009	12,500 ha
Cook et al. 2006	13,300 ha
Cox et al. 2004	6,475 ha
Cox et al. 2005	6,475 ha
Cram et al. 2002	>60,000 ha
Cram et al. 2006	60,000 ha
DeMaso et all. 1997	6,475 ha
Dunham et al. 2014	120,000 ha
Duren et al. 2011	State of Delaware
Flock et al. 2012	6,480 ha
Godbois et al. 2003	11,700 ha
Godbois et al. 2004	11,700 ha
Hall and Silvy 2006	9,500 ha
Lohr et al. 2011	12,500 ha
Lusk et al. 2005	6,475 ha
Masters et al. 2006	60,000 ha
Michener et al. 1997	11,500 ha
Miley and Lichtler 2006	42,430 ha
Perez et al. 2002	13,760 ha
Peterson et al. 1997	15,500 ha
Rader et al. 2007*b*	15,000 ha
Rader et al. 2011	15,000 ha

Table 1. Continued.

Reference	Study area
Ransom et al. 2008	12,000 ha
Rolland et al. 2011	26,799 ha
Sisson et al. 2006	20,000 ha
Terhune et al. 2006*a*	8,490 ha
Terhune et al. 2006*c*	12,980 ha
Terhune et al. 2008	8,490 ha
Townsend et al. 2001	6,475 ha
Townsend et al. 2003	6,475 ha
Turner et al. 2008	12,000 ha
Wellendorf et al. 2002	6,084 ha
Wellendorf et al. 2004	6,084 ha
Williams et al. 2012	12,500 ha
Region	
Bridges et al. 2002	Ecoregion
Evans et al. 2013	Eastern and Central U.S.
Hernandez et al. 2002*b*	Ecoregion
Lusk et al. 2001	State of Oklahoma[b]
Lusk et al. 2006*b*	Ecoregion
Lusk et al. 2007	Ecoregion
Peterson et al. 2002	Eastern and Central U.S.
Roseberry et al. 1998	State of Illinois
Scott et al. 2012	Ecoregion
Thogmartin et al. 2002	Southern Illinois
Tri et al. 2012	9,000,000 ha
Twedt et al. 2007	21,000,000 ha
Veech 2006	Eastern and Central U.S.
Weber and Roseberry 2002	11 Illinois counties
Williams et al. 2003*a*	State of Kansas

[a] Converted from county descriptions.

[b] Excluding Oklahoma and Tulsa counties.

programs have met with success (McKenzie et al. 2015), published research has not effectively addressed this issue and restoration of large habitat patches may not be a viable option in all cases. For one, much of the historical bobwhite habitat has been repurposed, often for agriculture and related industries, sometimes for afforestation (Crosby et al. 2015); displacing highly productive agricultural settlements for the sake of restoring bobwhite habitat is neither logically sound nor economically advisable (Peterson et al. 1997, Veech 2006). Still, landscapes wherein bobwhite habitat occurs primarily as patches are not necessarily beyond salvaging. Although mainly associated with grassland, scrubland, and pine (*Pinus* sp.) forest, bobwhites make use of several different kinds of habitat, and apparent "slack" in patch configuration could be beneficial (Guthery 1999). However, severe fragmentation may not be as easily navigated and other solutions must be found.

Fragmentation is a limiting factor to both population size and gene flow (Segelbacher et al. 2010, Robert 2011) and research increasingly supports the notion that observable effects of fragmentation are influenced by both temporal and geographic scale (Stephens et al. 2004, Smith et al. 2011, Reino et al. 2013). The importance of connectivity among habitat patches has been enumerated throughout conservation literature (Taylor et al. 1993, Metzger and Decamps 1997, Pascual-Horta and Saura 2006, Foster et al. 2016). However, studies of how bobwhites navigate fragmented habitat are few and it is evident that more research should be conducted in this area (Fies et al. 2002, Terhune et al. 2010, Scott et al. 2012).

One technique that has been proposed in the wider conservation literature to palliate the effects of fragmentation is to establish conservation corridors. In theory, corridors are an elegant solution to habitat fragmentation, though there has been considerable skepticism regarding their true efficacy (Simberloff and Cox 1987, Hobbs 1992, Harrison and Bruna 1999). Much of this skepticism arises from models of corridors (Falcy and Estades 2007) and from corridor experiments that neglect to account for the behavioral ecology and dispersal capabilities of the species they were meant to help (Chetkiewicz et al. 2006). Despite skepticism, research continues to pursue corridors as useful conservation tools and corridor design continues to be improved (Beier and Noss 1998, Chetkiewicz et al. 2006, Pascual-Hortal and Saura 2006). A model by Hudgens and Haddad (2003) predicted that corridors will most likely benefit slow-growing populations that experience high mortality rates when traversing matrix habitat, and stress that the benefits of corridors depend on the temporal scale of conservation. A model by Falcy and Estades (2007) demonstrated that habitat patch enlargement is preferable to corridor construction, but corridors may be useful in connecting larger but spatially distant habitat patches or in patches where enlargement is not possible. The use of corridors in bobwhite habitat management has been explored primarily at the local scale with field borders (Palmer et al. 2005, Riddle et al. 2008, Piispanen and Riddle 2012), with the exception of a study by Bowling et al. (2014), which both assessed the influence of field borders on bobwhite abundance and characterized landscape surrounding field borders. Studies utilizing large corridors have not been published. Determining whether or not corridors would be an effective management tool for bobwhites requires further study. Even if corridors are deemed not a viable conservation tool for bobwhites, more research should be focused on the value and increase of connectivity in the landscape of bobwhite habitat.

Ecological Processes

Scale of study and management often hinge on the population dynamics of a species. Bobwhites exhibit *r*-selective reproductive strategies with immense reproductive capabilities (Halley et al. 2014), capable of producing large clutches and multiple-broods during the breeding season (Hernandez and Peterson 2007). These factors result in bobwhite populations that exhibit a yearly boom–bust phenomenon, typically associated with environmental factors such as precipitation (Hernandez et al. 2005, Hernandez and Peterson 2007). Populations display drastic seasonal fluctuations, with unexploited populations of bobwhite quail sustaining calculated annual losses of 56% (Guthery et al. 2000) and hunted populations experiencing losses as great at 80% (Brennan 1991). The cyclic nature of bobwhite-boom bust dynamics has been observed at the regional level on large temporal scales (Thogmartin et al. 2002, Williams et al. 2003*a,* Lusk et al. 2007). Markedly few studies consider range-wide trends in bobwhite population ecology and dynamics (e.g., Parent et al. 2012). Most estimates of seasonal loss and fluctuations across years are based on studies performed at ranch-level. The possibility that stable populations of quail are larger and exist at greater spatial scales than are currently under study has the potential to change what we know about bobwhite population dynamics.

Population dynamics of most species are affected significantly by habitat loss and fragmentation. Bobwhite quail are no exception (Terhune et al. 2010) and it may be useful to apply principles from island biogeography to examine fragmented populations (Sands et al. 2012*b*). Smaller, more isolated, and more fragmented patches of habitat are likely to support populations more prone to extinction (Harrison and Bruna 1999). Proximity of biological islands (i.e., habitat patches) is critical because more closely grouped fragments may allow species to exhibit metapopulation dynamics. Metapopulation theory postulates that dispersal by individuals from one subpopulation to another will increase the viability and persistence of the metapopulation and that the local extinction or deterioration of one subpopulation can be recovered by individuals from nearby subpopulations (Stacey et al. 1997, Harrison and Bruna 1999, Martin et al. 2000, Hanski and Gaggiotti 2004). It is possible that our current estimations of what bobwhite populations can handle in regard to natural mortality and harvest pressure do not take metapopulation effects into account (Sands et al. 2012*b*). That is, a local population that sustains an annual mortality rate of 80% may only be able to do so because individuals from nearby subpopulations replenish the diminished population (source–sink dynamics). Metapopulation dynamics of this kind may not be seen at a ranch level examining a single patch of habitat. This presents a problem for bobwhite research performed at the ranch level because these habitat patches may be too small to support stable populations, given useable space and density-dependence. Bobwhite demographic patterns and characteristics have been studied using life stage analysis (LSA) models, which provide vital insight into factors that most strongly affect mortality and population persistence (Sandercock et al. 2008, Gates et al. 2012, Williams et al. 2012). Life-stage analysis models are useful in that they can provide demographic parameters for species about which little is known, in comparison with population viability analysis models (PVA), which generally work best for species about which much is known (Boyce 1992, Williams et al. 2012). However, because LSA models are often based on local data, they may not be capturing the entire picture.

Bobwhites have historically been regarded as a generally sedentary species. Though dispersal behavior across shorter distances is commonly observed, great dispersals by individuals are thought to be rare (Townsend et al. 2003). However, there is some evidence that bobwhite commonly disperse over large distances during the spring (Fies et al. 2002, Liberati and Gates 2012). Dispersal frequency appears to increase with increased habitat fragmentation (Fies et al. 2002), lending support to the notion that dispersal occurs as a result of the unavailability of suitable habitat, either because of saturation (reaching density-threshold) or habitat changes rendering the habitat unsuitable. In such a case, it has been observed that dispersing bobwhites are also more likely to survive than nondispersers during the breeding season (Townsend et al. 2003). Unsurprisingly, survival among dispersers is correlated with dispersal distance, and distance–survival relationships alternate during breeding vs. nonbreeding seasons (Lohr et al. 2011). Though dispersal appears to have survival benefits, it also poses mortality risks because matrix habitat (habitat not suitable to the species) must be traversed, and predation may be more likely in the matrix for species predated by relatively more mobile generalists (Wilcove 1985, Gehring and Swihart 2003, Ryall and Fahrig 2006). It is possible that, in ideal habitat conditions, bobwhites are completely sedentary but habitat fragmentation has altered their behavior. Alternatively, Berkman et al. (2013*b*) hypothesized that bobwhites may not be as sedentary as we have been led to believe, but that their tendencies toward longer dispersal have been hampered by the sparsity of suitable habitat. To reiterate an earlier point, it is evident that more studies should examine the movements and population dynamics of bobwhites because habitat degradation may have, by this point, completely precluded normal dispersal and population behavior, an assertion that has been corroborated elsewhere (Liberati and Gates 2012, Sands et al. 2012*b*). Small-scale research may not be capturing such phenomena, hindering both our understanding of bobwhite dispersal behavior and, consequently, population dynamics.

Expanding population dynamics studies to include landscape genetics and metapopulations.—Improving our understanding of bobwhite population dynamics is critical to enhancing the efficacy of broad-scale management. For most existing studies focusing on population dynamics and natural movements of bobwhites, radiotelemetry has been employed; however, this method has been called into question as seriously underestimating survivorship (Osborne et al. 1997, Cox et al. 2004) and potentially handicapping radiotagged birds (Guthery and Lusk 2004). If telemetry devices are cumbersome enough to preclude normal movements or decrease survivorship, experiments utilizing current telemetry devices may not be able to accurately study large-scale dispersal. Improvement of radiotelemetry devices is recommended to aid this purpose. Furthermore, although radiotelemetry has provided insightful demographic information about bobwhite populations (Williams et al. 2000, Scott et al. 2012), it reveals little about how these individuals contribute to the genetic fitness of a population, which is important for population persistence (Reed and Frankham 2003). An alternative approach to monitoring population dynamics may be found in the nascent field of landscape genetics, which seeks to understand how landscape features affect gene flow; this, in turn, can be used to make valuable inferences about ecological processes of populations (Holderegger and Wagner 2006).

Tools and methods of genetic study have become critical to modern conservation science. Studies of population genetics have been used in combination with demographic patterns to estimate viable population sizes (Lande 1988, Nunney and Campbell 1993), and genomic studies of ancient DNA have yielded valuable insights into the prehistoric population dynamics of species, including those of the bobwhite (Halley et al. 2014). However, population genetics studies rely on the supposition of large populations and spatial symmetry and do not incorporate detailed life-history data into their analyses (Segelbacher et al. 2010). In this respect, landscape genetic studies may be more useful for examining bobwhite populations, especially because they account for the effects of landscape features on genetic structure and thus gene flow. Information about genetic structure with relation to landscape features may be used with demographic information to improve the accuracy of models (e.g., LSA or PVA) and help determine the overall fitness of a population (Nunney and Campbell 1993, Robert 2011). Landscape genetics is showing increasing promise in the management of threatened species, and several studies of its practical application are evident in literature (Epps et al. 2005, Vignieri 2005, Riley et al. 2006, Segelbacher et al. 2008). However, relatively few studies have examined bobwhites in the context of landscape genetics. A single example for bobwhites exists in 2 studies by Berkman et al. (2013*a, b*) based on the same metapopulation of bobwhites.

The first study by Berkman et al. (2013*b*) examined the effects of a single landscape feature (highways) on gene flow in metapopulation of bobwhites in southern Illinois. Interestingly, this study found that highways did not present a significant barrier to gene flow; rather, geographic distance between subpopulations was cited as the factor contributing most to genetic differentiation (Berkman et al. 2013*b*). The second study by Berkman et al. (2013*a*) attempted to determine overall genetic structure in and among these same subpopulations. In this analysis, Berkman et al. (2013*a*) found that an isolation-by-distance pattern was not apparent for the subpopulations and that the subpopulations exhibited a low amount of genetic structure. The authors postulated that their results indicated early patterns of genetic drift resulting from the recently agriculturally modified landscape (Berkman et al. 2013*a*). Bobwhites are not regarded to be proficient dispersers, so one might expect to see an isolation-by-distance pattern in the genetic structure of several subpopulations (Townsend et al. 2003, Haig et al. 2011). Though a low amount of genetic structure was observed overall, significant genetic structure was apparent at distances up to 11.4 km; the authors suggested that metapopulation processes of extinction and colonization could have been responsible for the low genetic structure, and additionally suggested that the structure observed up to 11.4 km was due to difficulties in dispersal. The recommendation from both studies was for larger, contiguous tracts of habitat within dispersal range (Berkman et al. 2013*a, b*). These recommendations are corroborated by modeling efforts such as those conducted by Ovaskainen et al. (2002), which found that the equilibrium of metapopulation size was affected by the spatial connectivity of patches and that patches should be well within dispersal distance of a species.

Studies such as these based on landscape genetics are, by themselves, far from plenary. By nature, the models produced by landscape genetics have limitations (Segelbacher et al. 2010, Berkman et al. 2013*a, b*). However, the analyses by Berkman et al. (2013*a, b*) provide an example of how landscape genetics can be used to make landscape management decisions, and they lend further credence to the idea that habitat management for bobwhites must be undertaken on a landscape-scale with a conscious effort to acknowledge the impact of landscape features on bobwhite dispersal and, thus, the genetic fitness of populations. Landscape genetics should be combined with improved telemetry equipment to make inferences and predictions about demographic patterns and connectivity for management decisions about bobwhite conservation (Haig et al. 2011, Keller 2015).

CONCLUSION

We conclude that there is a possible, if not probable, disconnect between the scales of management and research practices for the conservation of northern bobwhites. Small-scale research is likely insufficient to answer 2 of the most pressing questions in bobwhite conservation: 1) how much space a viable population requires, and 2) what ecological processes influence the persistence of local populations, and how such processes are affected by landscape features. Future research should endeavor to address the northern bobwhite decline at a large scale and utilize technologies, such as landscape genetics, that have the power to answer those questions.

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EFFECTS OF TANGLEHEAD EXPANSION ON BOBWHITE HABITAT USE IN SOUTH TEXAS

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ABSTRACT

Usable space for northern bobwhite (*Colinus virginianus*) has been reduced across a large portion of South Texas rangelands due to the spread of non-native, invasive grasses. A native grass, tanglehead (*Heteropogon contortus*) has rapidly expanded its dominance in the western Sand Sheet of South Texas within the last 10-15 years. It has formed high-density monocultures, similar to non-native grasses, which are associated with losses of forb and grass diversity as well as bare ground, which are key components of bobwhite habitat. The objectives of our research were to 1) determine selection-avoidance of habitat features by bobwhites, and 2) determine the effects of tanglehead cover on vegetation characteristics. We detected 488 coveys across 20,103 ha on helicopter surveys conducted December 2014 in South Texas. We measured 6 vegetation characterstics (grass and forb species richness, vegetation height, woody-plant cover, tanglehead cover, and non-native grass cover) at all covey detections and an equal number of random locations. We developed continuous selection ratios based on probability density functions of used and random points derived using Simple Saddlepoint Approximations to determine habitat selection by bobwhites. We also used quantile regression at the 10th, 50th, and 90th quantiles to determine relationships between tanglehead and vegetation factors. Bobwhite avoided areas of high canopy cover (>20%) of all invasive grasses measured. Brush cover was selected for up to 47%, after which it was avoided. We found significant negative relationships between tanglehead cover and forb and grass species richness, bare ground, and shrub cover, and a positive relationship with vegetation height at all quantiles modeled. Our results demonstrate the negative effects of increased tanglehead cover on native rangeland habitats. Further expansion by tanglehead has the potential to significantly reduce usable space for bobwhites in South Texas.

Citation: Edwards, J. T., F. Hernández, D. B. Wester, L. A. Brennan, C. J. Parent, and F. C. Bryant. 2017. Effects of tanglehead expansion on bobwhite habitat use in South Texas. National Quail Symposium Proceedings 8:132.

Key words: usable space, tanglehead, monoculture, quantile, selection, avoidance

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HABITAT SPACE USED BY NORTHERN BOBWHITES AND TEXAS TORTOISES ON SOUTH TEXAS RANGELANDS

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ABSTRACT

South Texas rangelands are increasingly managed for recreational hunting, particularly northern bobwhite (*Colinus virgianus*). Effects of habitat management for game species on non-game species are largely unknown. Large private ranches used for recreational hunting could also provide habitat for the threatened Texas tortoise (*Gopherus berlandieri*). We studied habitat use of Texas tortoises and northern bobwhites on a private ranch in South Texas that undergoes active habitat management. In 2015, tortoises (n=12) and bobwhite hens (n=42) were tracked during their active and breeding seasons, respectively, with radio-telemetry. Satellite images were analyzed using ArcGIS 10.3 to delineate habitat through unsupervised classification for relevant habitat categories. Habitats were delineated based on reflectance. Differences in percent habitat composition of observed and random home ranges (100% Minimum Convex Polygon) of tortoises were not significant, but were significant for quail in 3 of 5 habitat categories in only 1 of 2 pastures. These observed quail home ranges included more areas corresponding to light woody cover and moderate herbaceous cover and fewer areas corresponding to sparsely vegetated or bare ground than random home ranges. Tortoise home ranges included more areas with woody brush cover than bobwhite home ranges. Bobwhite home ranges included more areas associated with moderate grass and herbaceous cover than tortoises. This study will continue in 2016 and will include more quail home ranges in areas with tortoises. This research seeks to determine the compatibility of managing for recreational hunting while maintaining landscape characteristics important to Texas tortoises.

Citation: Couvillon, R. O., L. A. Brennan, F. Hernández, B. M. Ballard, and T.V. Dailey. 2017. Habitat space used by northern bobwhites and Texas tortoises on south texas rangelands. National Quail Symposium Proceedings 8:133.

Key words: northern bobwhite, Texas tortoise, *Colinus virgianus*, *Gopherus berlandieri*, habitat compatibility, habitat use, non-game, sympatry

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NATIONAL BOBWHITE CONSERVATION INITIATIVE FOCUS AREA MONITORING IN THE 2C FOCUS AREA, MISSOURI

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ABSTRACT

The Missouri Department of Conservation (MDC) began establishing Quail Focus Areas (QFAs) on private lands in 2004. The goal of QFAs is to increase and expand quail habitat management efforts at a larger scale. Because most (93%) of Missouri's landscape is in private ownership, habitat improvement programs on private lands have greater potential to impact quail populations than on public lands alone. In spring of 2013, a group of MDC staff and Quail Forever biologists began monitoring bobwhite quail (*Colinus virginianus*) and songbirds in a portion of the 2C QFA in Carroll County, Missouri as well as in a control area (without habitat management for bobwhite). This effort is part of the Coordinated Implementation Plan developed by the National Bobwhite Technical Committee as a part of the National Bobwhite Conservation Initiative. The goal of the monitoring plan is to document within 5-10 years, if quail habitat management can achieve sustainable bobwhite populations. We selected a 5,200-acre (2014-ha) portion of the 2C QFA where habitat management for quail has been conducted through efforts by landowners, MDC staff and Quail Forever volunteers. Point transect surveys are conducted at 48 250-m radius points in the spring for bobwhite and other songbirds and at 12 500-m radius points in the fall for bobwhite coveys. In 2013, we heard three times more quail in the focus area, compared to the control area. We heard between 2 and 3 times more dickcissels (*Spiza americana*), eastern meadowlarks (*Sturnella magna*), and field sparrows (*Spizella pusilla*) in the focus area versus the control, demonstrating that habitat management for quail also benefits a variety of other grassland bird species. During the spring of 2014, we heard a total of 426 bobwhites in the focus area compared to only 78 in the control area. In fall 2013, we heard an average of 2.7 coveys per point in the focus area, and only 0.3 coveys per point in the control area. In fall 2014, we heard an average of 3.9 coveys per point inside the focus area and 1.8 coveys per point in the control area. Additional data from 2015 will be presented. These surveys continue to show that habitat management for bobwhite continues to benefit other grassland bird species.

Citation: Emmerich, B. A., W. T. White, and E. L. Metcalf. 2017. National bobwhite conservation initiative focus area monitoring in the 2c focus area, Missouri. National Quail Symposium Proceedings 8:134.

Key words: *Colinus virginianus*, point transect surveys, focus area, monitoring, private land, Missouri, northern bobwhite

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RESPONSE OF NORTHERN BOBWHITE TO LONGLEAF PINE ECOSYSTEM ENHANCEMENT THROUGH THE STATE WILDLIFE GRANT PROGRAM

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ABSTRACT

The State Wildlife Grant (SWG) program provides funding through the U.S. Fish and Wildlife Service to benefit species of greatest conservation need as recognized by State Comprehensive Wildlife Conservation Plans (SCWCPs). The northern bobwhite (*Colinus virginianus*) is an important game bird that shares habitat overlap with many priority species identified within SCWCPs. Specifically, in longleaf pine forests the Federally Threatened gopher tortoise (*Gopherus polyphemus*) is dependent upon similar understory conditions as are bobwhite. As part of a multistate competitive SWG funded to enhance gopher tortoise habitat, we applied selective herbicide treatments and prescribed fire to longleaf pine forests representing approximately 20% of a public Wildlife Management Area in Mississippi. Our objectives were to rapidly restore forest understory indicative of functional longleaf ecosystems, and increase populations of high priority wildlife, including bobwhite. We used line transect sampling and breeding season call counts to respectively document the response of vegetation and bobwhite to treatments. Coverage of woody shrubs was reduced, whereas coverage of herbaceous plants and grasses increased following treatments. Use of occupancy modeling suggested that bobwhite breeding season colonization of treated areas was increased over that of control areas. Our work documents significance of nongame habitat enhancement for an important game species, and demonstrates nontraditional use of funding for bobwhite management.

Citation: Butler, A. B., J. P. Gruchy, R. G. Hamrick, and M. Elliott. 2017. Response of northern bobwhite to longleaf pine ecosystem enhancement through the state wildlife grant program. National Quail Symposium Proceedings 8:135.

Key words: northern bobwhite, *Colinus virginianus*, State Wildlife Grants, longleaf pine, *Pinus palustris*, Gopher tortoise, *Gopherus polyphemus*, occupancy modeling

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UNCERTAINTY AND THE ENTANGLEMENT OF HABITAT LOSS AND FRAGMENTATION EFFECTS IN THE MANAGEMENT OF NORTHERN BOBWHITE

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ABSTRACT

There is a need to understand the effects of habitat loss and fragmentation on northern bobwhite (*Colinus virginianus*) and other grassland bird species and relate this to conservation action and delivery, especially in areas of intensive anthropogenic development. Through our research, we investigated the factors contributing to habitat loss and fragmentation in order to prioritize management within the Gulf Coast Prairie Landscape Conservation Cooperative (GCP LCC) region of Texas, USA. For this geographic region, we completed these objectives: analyzed grassland bird habitat loss and fragmentation resulting from oil and gas development, which has become especially rapid in this region beginning in 2008, projected future habitat loss under possible future economic scenarios, modeled the outcomes of potential management alternatives, and identified drivers of habitat loss and fragmentation to direct management action toward minimizing threats to high-risk habitats. Using a modeling approach, we identified suitable bobwhite habitat and prioritized high-risk areas, particularly focusing on the best candidate areas for successful restoration. Briefly, point count data were related to patch- and landscape-level habitat characteristics using a modeling technique that formally estimated the scale of the landscape effect on bobwhite abundance. Thereafter, we identified possible management alternatives with the guidance of the GCP LCC and other stakeholders and modeled the consequences of these alternatives. Using results from this modeling, we produced an extinction risk map for northern bobwhite in this region. Our research adds to the understanding of the relationship between northern bobwhite populations and the expansion of energy extraction and also uses modeling informed by data to support a decision-making framework that incorporates uncertainty about this system to prioritize the conservation of high-risk and high-value areas of bobwhite habitat.

Citation: Cline, M. H., R. Chandler, C. T. Moore, and J. A. Martin. 2017. Uncertainty and the entanglement of habitat loss and fragmentation effects in the management of northern bobwhite. National Quail Symposium Proceedings 8:136.

Key words: *Colinus virginianus*, habitat loss and fragmentation, oil and gas development, northern bobwhite, grassland birds, management alternatives, spatial modeling

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THE LAW OF INTERSPERSION AND THE PRINCIPLE OF EDGE: OLD ARGUMENTS AND A NEW SYNTHESIS

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ABSTRACT

Leopold's interspersion hypothesis has experienced fluctuating acceptance, opposition and neglect due to its unintentional ambiguous description and seemingly simplistically universal application. Originally developed to describe the positive association between animal density and habitat heterogeneity in the landscape, the hypothesis has been mischaracterized as the principle of edge resulting from Guthery and Bingham's (1992) assertion that the interspersion hypothesis could be modeled by the amount of 'high contrast' edge and that edge density and interspersion were synonymous. We contend that Leopold's original intention was not to promote more edge density is always better but rather to promote interspersion of habitat types within landscapes suitable for bobwhite. We argue that edge density and interspersion are different metrics to describe landscape configuration but are incorrectly used interchangeably. These metrics reflect two unique hypotheses regarding bobwhite relationships with landscape structure. We used a northern bobwhite (*Colinus virginianus*) monitoring dataset to demonstrate the importance of the proper use of edge density and interspersion metrics. We modeled bobwhite abundance at 160 sites across 6 years using an open N-mixture model. We used Fragstats to calculate edge density and interspersion at the landscape scale. These metrics were not correlated ($r < .10$) indicating they describe unique aspects of configurational heterogeneity. Both metrics had positive but varying effects on bobwhite abundance. We recommend scientists have explicit *a priori* hypothesis regarding the differential effects of edge density and interspersion.

Citation: McConnell, M.D., L. W. Burger, Jr. and J. A. Martin. 2017. The law of interspersion and the principle of edge: old arguments and a new synthesis. National Quail Symposium Proceedings 8:137.

Key words: bobwhite, interspersion, edge density, landscape ecology, principle of edge

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AUTOMATED IDENTIFICATION AND MAPPING OF WOODY HABITAT USING DIGITAL ORTHO IMAGERY

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) restoration efforts operate at multiple spatial scales, from landscape (regional) levels to farm level (local). Choosing proper data sources, analysis techniques, and accounting for differences in scale (minimum mapping unit) between sources are critical first steps to successfully delivering habitat information useful for broad regional planning efforts and site specific research and management activities. To this end, we compared 3 methods of creating a habitat map and associated data: National Landcover Dataset (NLCD) 2006, hand digitized from 2010 National Agriculture Imagery Program (NAIP) imagery, and an Interactive Supervised Classification of 1-m NAIP imagery using ArcGIS 10.1. We analyzed a 3,660-ha portion of Peabody Wildlife Management Area in Muhlenberg and Ohio counties in west central Kentucky. We also compared percent cover of forest canopy closure using 2011 NLCD Percent Canopy Closure along with 10-m and 30-m aggregated datasets derived from image classification. Office inspection of aerial imagery and field verification yielded a 94% positive identification of woody vegetation. We found good agreement between NLCD 2006 and Image Classification for habitat classes. Hand digitizing did not compare well and this method is not recommended for creating digital habitat data. Percent Canopy closure yielded similar results between data sources. We found the smaller pixel size of the 10-m aggregate data to better identify small woody patches in open matrix. Use of 30-m national datasets to compare basic habitat across large areas is well warranted. Site specific research and management activities will benefit from image classification of 1-m imagery. We recommend additional research into the relationship between varying pixel size and habitat classification.

Citation: Wethington, M. K. 2017. Automated identification and mapping of woody habitat using digital ortho imagery. National Quail Symposium Proceedings 8:138.

Key words: National Agriculture Imagery Program (NAIP) ortho imagery, habitat mapping, National Landcover Dataset 2006, Kentucky Canopy Closure 2011, image classification toolbar, aggregate tool, interactive supervised classification

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HOW MANY ARE THERE? ESTIMATING THE NORTH AMERICAN NORTHERN BOBWHITE POPULATION SIZE FOR CONSERVATION PLANNING PURPOSES

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ABSTRACT

Three bird habitat Joint Ventures, Gulf Coast, Oaks & Prairies, and Rio Grande, developed a method to set spring population and habitat objectives for northern bobwhite (*Colinus virginianus*) populations in four Bird Conservation Regions (BCRs). The method requires an estimate of current population size that can be stepped down to the management unit of interest. Several methods have been designed to estimate range-wide populations over the past two decades for fall (post-breeding) and spring (pre-breeding). The 2002 Northern Bobwhite Conservation Initiative (NBCI) provided an estimate of 6,714,000 birds for the 1999 breeding population. The 2007 Partners in Flight (PIF) Population Estimates database provided a spring population estimate of 7,600,000 based on Breeding Bird Survey (BBS) densities. The NBCI 2011 revision population estimate, using BCR-specific Estimated Densities and habitat acreages, summed to greater than 26,000,000 individuals for fall population. The current PIF (2013) Population Estimates database includes 5,800,000 individuals as a global (spring) population estimate, and cites the NBCI. This estimate may result from application of the range-wide BBS trend estimate from 1982-1999 (3.8%) to the 2002 NBCI spring estimate. This produces a 2003 population estimate of ~5,800,000, which may have been substituted for the BBS-based estimate used in the 2004 PIF North American Landbird Conservation Plan. Finally, a recent unpublished estimate based upon the BBS-based PIF calculated estimate suggests a population of almost 18,000,000 in the U.S. and Canada. This value excludes birds in Mexico, estimated to comprise approximately 15.6% of the global population. We compared PIF estimates with the 2011 NBCI estimate. While there is some correlation regarding population density estimates at the BCR level, there is considerable disparity between overall population estimates between the two documents. The bird conservation community would benefit from an examination of northern bobwhite population estimates, to improve accuracy of spring population and habitat objectives.

Citation: Giocomo, J., W. Vermillion, S. DeMaso, and A. Panjabi. 2017. How many are there? Estimating the North American northern bobwhite population size for conservation planning purposes. National Quail Symposium Proceedings 8:139.

Key words: *Colinus virginianus,* habitat objective, joint venture, Partners in Flight, population estimate, population objective, northern bobwhite, Northern Bobwhite Conservation Initiative

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A METHOD FOR SETTING NORTHERN BOBWHITE POPULATION AND HABITAT OBJECTIVES FOR LARGE LANDSCAPE PARTNERSHIPS

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ABSTRACT

Population and habitat objectives are the foundation for many conservation actions. Often objectives set at one scale are difficult to translate to larger or smaller scales. Three bird habitat Joint Ventures, Gulf Coast, Oaks & Prairies, and Rio Grande, working cooperatively with the Gulf Coast Prairie Landscape Conservation Cooperative, have a common objective to stabilize northern bobwhite (*Colinus virginianus*) populations in four Bird Conservation Regions. We cooperatively developed a method using the North American Breeding Bird Survey trend for several scenarios with different time horizons (10-, 20-, 30-year, or longer), the spring home range size, and the per acre cost of habitat management actions, to set spring population and habitat objectives and projected costs. The spring population objectives can easily be converted to fall population objectives using the percent summer gain. We provide an example of how three Joint Ventures could use this methodology to set bobwhite objectives within their geographies and then scale those objectives up to the next larger geography, a Landscape Conservation Cooperative geography. This methodology can be used by other multi-state partnerships (e.g., Joint Ventures and Landscape Conservation Cooperatives) across the bobwhite range to provide the bobwhite conservation community meaningful objectives at regional and national scales.

Citation: Giocomo, J., W. Vermillion, S. DeMaso, B. Wilson, J. Hayes, K. Gee, J. Franco, A. Roberson, R. Perez, J. Raasch, B. Bartush, B. Kahler. 2017. A method for setting northern bobwhite population and habitat objectives for large landscape partnerships. National Quail Symposium Proceedings 8:140–141.

Key words: *Colinus virginianus,* habitat objective, joint venture, landscape conservation cooperative, partnership, population objective, northern bobwhite

DATA-DRIVEN PLANNING FOR THE CONSERVATION OF GRASSLAND BIRDS IN THE CENTRAL HARDWOODS BIRD CONSERVATION REGION

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ABSTRACT

The Central Hardwoods Joint Venture held two workshops in 2006 to delineate bobwhite focus areas across the Central Hardwoods Bird Conservation Region (BCR) for targeting on-the-ground conservation efforts. From 2008 – 2012, we conducted randomized sets of point counts within counties containing bobwhite focal areas to assess the efficacy of that method for monitoring grassland birds within focal areas, and to assess relationships of conservation practices with bird species occupancy and abundance. We collected data on nine species of Partners in Flight priority species, including northern bobwhite (*Colinus virginianus*). Land cover types within a 200-m buffer of each point were derived from year National Agricultural Statistics Service data, and information related to the location of conservation practices deemed beneficial to grassland birds was attained from the National Resources Conservation Service. We fit occupancy and abundance models for each species using Akaike's Information Criterion adjusted for small sample sizes. We then used the model covariates to map predicted abundances of three species, northern bobwhite, eastern meadowlark (*Sturnella magna*), and Henslow's sparrow (*Ammodramus henslowii*) across the BCR. The spatial patterns of predicted abundance varied among species, suggesting that focus areas should be somewhat species-specific. We will use data collected around the nests of each species at Ft. Campbell, a military base straddling the Kentucky-Tennessee border where grassland management has occurred at relatively large scales over more than two decades, to assess the with-in patch structure preferred by each species to develop grazing practices that will result in the desired structure for the species suite.

Citation: Joos, C. J., J. A. Fitzgerald, C. M. Lituma, J. J. Giocomo, and L. Heggemann. 2017. Data-driven planning for the conservation of grassland birds in the Central Hardwoods Bird Conservation Region. National Quail Symposium Proceedings 8:142.

Key words: *Colinus virginianus, Sturnella magna*, *Ammodramus henslowii*, Central Hardwoods Bird Conservation Region, grassland birds

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LANDSCAPE-SCALE GEOSPATIAL ASSESSMENT OF OPEN PINE AND NATURAL GRASSLAND CONDITION FOR NORTHERN BOBWHITE IN THE GULF COASTAL PLAINS AND OZARKS

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ABSTRACT

The National Bobwhite Conservation Initiative 2.0 (NBCI) suggests >13 million acres of pine forests and >600,000 acres of grasslands have high potential for northern bobwhite (*Colinus virginianus*) conservation in the Southeast. The Gulf Coastal Plains and Ozarks Landscape Conservation Cooperative (LCC) identifies northern bobwhite as one of 15 indicator species for open pine/woodland/savanna and grassland/prairie ecological systems, and describes specific habitat conditions considered desirable as measurable landscape endpoints in each system as part of an Integrated Science Agenda (ISA). The ISA suggests bobwhite are limited by the habitat characteristics associated with basal area and canopy cover in pine systems, and patch size, vegetation density, bare ground, shrub cover, and warm-season grass density in grassland systems across the 180 million acre LCC. We conducted Rapid Ecological Assessments (REAs) of pine and grassland systems to describe where, how much, and in what condition the desired habitat conditions exist for each system. Using endpoint threshold values, the best available geospatial data, and a dichotomous decision tree approach, the pine and grassland REAs assigned per-pixel Condition Index Values (CIV) for the entire LCC. Results indicate 46% of the 48 million acres of pine or mixed-pine hardwood forests are in patches >600 acres with one other endpoint present, but only 0.2% (100,000 acres) reflect all desired open pine conditions. In the grassland system, 48% of the 32 million acres of grassland were characterized by the presence of at least one desired condition, with no areas meeting all desired conditions. In many cases, areas with high CIV scores overlap areas classified as high and medium land use opportunities in NBCI 2.0, suggesting continuity of these independent empirical and expert-driven assessments. Understanding the current condition of pine and grassland systems in concert with NBCI potential acreage targets can help refine management and population objectives in NBCI and LCC conservation planning.

Citation: Gray, T., K. Evans, and T. Jones-Farrand. 2017. Landscape-scale geospatial assessment of open pine and natural grassland condition for northern bobwhite in the Gulf Coastal Plains and Ozarks. National Quail Symposium Proceedings 8:143.

Key words: *Colinus virginianus*, desired forest conditions, ecological assessment, grassland, landscape conservation design, northern bobwhite, open pine, prairie

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IMPACTS OF HABITAT FRAGMENTATION ON NORTHERN BOBWHITES IN THE GULF COAST PRAIRIE LANDSCAPE CONSERVATION COOPERATIVE

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ABSTRACT

The northern bobwhite (*Colinus virginianus*) has experienced range wide declines over the last several decades, primarily due to loss and fragmentation of habitat. As populations decline, there is a need for understanding factors that impact bobwhite population persistence at local and regional spatial scales. Our goal was to assess changes in land use and their relationship to bobwhite declines at 3 different spatial scales (region, county, and home range) in Texas, Oklahoma, and Louisiana. We used North American Breeding Bird Survey (BBS) data from 1974-2014 to create abundance maps and trends. At the regional scale, we compared bobwhite abundance with road density (2000, 2010), human population (1970-2010), and land use (1974-2012). We then used the BBS data to identify counties with stable and declining bobwhite abundance, and then compared bobwhite abundance to land use at metapopulation (800-9600 ha) and home range scales (15 ha). Bobwhite populations decreased from 45.93 ± 1.01 birds/count in 1970 to 11.55 ± 0.64 birds/count in

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2012. as road density and human population increased. Pasture and other land increased, woodland was relatively stable, and cropland decreased in 2012. At the metapopulation level, declining populations had higher road density, more edge and patch area for pasture, and larger patches of cropland compared to stable populations. At the home range scale, declining populations had significantly fewer, and smaller, woody patches, more herbaceous habitat, and less bare ground. This study demonstrates that while on a small scale managers can provide woody cover and reduce cropland effects to support stable populations, the large-scale drivers of bobwhite decline, namely human population growth and the resulting loss of habitat, will be critical to quail management in the future.

Citation: Miller, K. S., L. A. Brennan, H. L. Perotto-Baldivieso, F. Hernández, E. D. Grahmann, A. Z. Okay, X. B. Wu, M. J. Peterson, H. Hannusch, J. Mata, and J. Robles. 2017. Impacts of habitat fragmentation on northern bobwhites in the Gulf Coast Prairie Landscape Conservation Cooperative. National Quail Symposium Proceedings 8:144–145.

Key words: Breeding Bird Survey, *Colinus virginianus*, habitat fragmentation, land use, northern bobwhite

UTILITY OF FINE RESOLUTION LAND COVER DATA FOR MODELING NORTHERN BOBWHITE ABUNDANCE IN THE OAKS AND PRAIRIES OF OKLAHOMA

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ABSTRACT

Management of northern bobwhite (*Colinus virginianus*) requires landscape-level planning to promote sustainable populations. Limitations in time and resources necessitate the use of large geographic datasets to efficiently evaluate habitat suitability across landscapes. Many such datasets, however, are limited by a lack of detailed and current information relevant to regional management efforts. To meet this need, regional partners recently released the Oklahoma Ecological Systems Mapping (OESM) product, which offers high spatial and thematic resolution vegetation data, current to 2015. We evaluated the utility of the new OESM product for modelling abundance of northern bobwhite and other grassland birds, relating percent cover types to bird survey data from the Oaks and Prairies Joint Venture. Using an information-theoretic approach (AIC), we compared the performance of OESM to the more widely known National Land Cover Dataset (NLCD). The OESM data provided information on 20 land cover types at 10-m resolution compared 7 types and 30-m resolution for NLCD. We conducted a total of 2,367 individual counts for breeding birds from May–July, 2014–2016, across 10 counties in the Oklahoma Oaks and Prairies ecoregion. We used generalized linear mixed models to control for random effects of year and AICc to evaluate model performance. OESM models vastly outperformed NLCD for 6/7 species (AIC weights >0.99). Northern bobwhite was the only species where NLCD was the highest performing model. These results suggest that, in contrast to other grassland species, added levels of habitat complexity do not inform our ability to model local bobwhite abundance.

Citation: Jaffe, N., T. O'Connell, and J. Giocomo. 2017. Utility of fine resolution land cover data for modeling northern bobwhite abundance in the oaks and prairies of Oklahoma. National Quail Symposium Proceedings 8:146.

Key words: northern bobwhite, habitat complexity, landcover, vegetation, map resolution, grassland birds, Oaks and Prairies

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EVALUATING TEMPORAL DIFFERENCES IN LAND COVER: IMPLICATIONS FOR MANAGING BOBWHITE AT THE LANDSCAPE SCALE IN VIRGINIA

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) populations have declined substantially across large portions of their range. A number of factors may be contributing to that decline including disease, predation, pesticides, and habitat loss. Of these, habitat loss has emerged as the primary factor. Habitat loss has occurred at large and small scales. It is relatively easy to evaluate bobwhite habitat at the micro scale, but evaluating habitat change at the landscape scale is difficult. The goal of this pilot study was to evaluate a novel technique using aerial imagery and line transects to evaluate both contemporary and historic landscapes effectively, quantifying the differences observed to describe what changes, if any, occurred through time. Contemporary photos were available through the 2013 Virginia Base Mapping Program. Historic photos were obtained via United States Geological Survey (1967 – 1969). Two Virginia Quail recovery Initiative focal counties were chosen for the study, Halifax (south central Piedmont) and Sussex (southeastern Coastal Plain). A 12-class habitat categorization system was developed to use in analysis. We developed a technique that allowed photo interpreters to identify and delineate features at a large scale ($>$ 1:6000) over a wide geographic area. Thirty-five to forty transects were evaluated for each site ($n = 7$). Favorable habitat decline observed ranged from -2% to -49%. Favorable edge decreased through time in four of five sites in Halifax County. Favorable edge increased dramatically within both Sussex County sites, particularly in the bobwhite focal area. Overall, habitat appears to have improved in Sussex County, and declined significantly in Halifax County. Habitats differed both through time and across the landscape. The largest habitat change noted was conversion from field to forest, predominantly pine. We feel this landscape scale habitat analysis technique holds much promise across the bobwhite's range.

Citation: Klopfer, S. D., D. A. Cross, K. Mcguckin, J. E. Howell, And K. M. Puckett. 2017. Evaluating temporal differences in land cover: implications for managing bobwhite at the landscape scale in Virginia. National Quail Symposium Proceedings 8:147.

Key words: *Colinus virginianus,* landscape, Halifax County, Sussex County, habitat creation, historic, contemporary, aerial photos, line transects, novel technique

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RESPONSE OF GRASSLAND BIRDS TO AGRICULTURAL INTENSITY AT DIFFERENT SPATIAL SCALES IN TEXAS

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ABSTRACT

The decline in grassland birds is often associated with habitat loss due to intensity of conversion to agricultural lands and the alterations of natural disturbances. We sought to identify agricultural effects at differing scales that correlate to Texas grassland bird abundance, especially northern bobwhite (*Colinus virginianus*). Ninety-five roadside routes were surveyed in 20 Texas counties ranging from the Oklahoma border to the coastal plains. We conducted point counts in May and June from 2013 to 2016. To estimate the coarse effects of agriculture on bird abundance at a county level, we used number of cattle and area of farmland used per crop type amongst other data from the National Agriculture Statistics Service (NASS, 2012) for analyses. For estimates at finer scales, including the scale of individual routes and points, we obtained annual agricultural data and GIS layers from the NASS. We determined the predictive ability of each agricultural type via linear models and stepwise selection. From 2013 to 2016, we detected 32,373 individual birds, including 5,329 northern bobwhite, from 150,423 point count surveys. Our preliminary results revealed that agriculture only affects a few species at a county level. The top models for rufous-crowned sparrows (*Aimophila ruficeps*) and field sparrows (*Spizella pusilla*) included only one predictor from the full model - the number of cattle per county ($R^2 = 0.10$; $R^2 = 0.29$). The top model for yellow-billed cuckoos (*Coccyzus americanus*) included cattle per county and year, while the best model was found for dickcissels (*Spiza americana*), which included year and the proportions of woodland agriculture and pasture ($R^2 = 0.23$; $R^2 = 0.33$). While our results may indicate that agriculture impacts some species on coarse scales, it appears that bobwhite are likely impacted only on smaller scales and further analysis will be needed to identify specific impacts of agriculture on these scales.

Citation: Matthews, A., M. C. Green, and J. Giocomo. 2017. Response of grassland birds to agricultural intensity at different spatial scales in Texas. National Quail Symposium Proceedings 8:148.

Key words: *Colinus virginianus*, northern bobwhite, *Spiza americana*, dickcissel, *Coccyzus americanus*, yellow-billed cuckoo, *Aimophila ruficeps*, rufous-crowned sparrow, *Spizella pusilla*, field sparrow, grassland birds, Texas, agriculture, abundance, scale

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PARTNERING FOR QUAIL IN SOUTH CAROLINA: A COOPERATIVE APPROACH MAKING A DIFFERENCE

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ABSTRACT

The National Bobwhite Conservation Initiative (NBCI) identified 15 national quail focal areas throughout the distribution of the northern bobwhite (*Colinus virginianus*) in June 2016. The first NBCI Focal Area on U.S. Forest Service System land emerged from the existing 16,200-hectare Indian Creek Woodland and Savanna Restoration Initiative (ICWSRI). The ICWSRI is an ongoing collaborative project involving partners from 10 agencies and organizations in the Piedmont of South Carolina. Cooperation among federal and state agencies, non-governmental organizations (NGO), and private landowners, combined with assistance programs such as the Environmental Quality Incentives Program (EQIP) have currently resulted in 2,547 hectares (1,600 hectares on private land and 947 hectares on public land) of improved habitat for wildlife species associated with pine woodlands and savannas. Data obtained through the Breeding Bird Survey, spring whistle counts, and fall covey counts suggest a correlation between woodland and savanna restoration and avian response across the ICWSRI area. Fall covey count minimum population estimates (birds/ha) ranged from 1/38 in 2008 to 1/7 in 2016. Spring whistle count population density estimates (birds/ha) ranged from 1/37 in 2009 to 1/6 in 2012. Although monitoring suggests an initial increase in bobwhite densities across the project area, it is imperative to continue involving existing and additional partners to increase habitat availability, connectivity, and quality for bobwhite and associated species. Collaborative efforts and partnerships across ownership boundaries are necessary to increase bobwhite populations on a landscape scale. The Indian Creek project has effectively involved efforts from federal, state, NGO, and private partners to restore and improve bobwhite habitat and may serve as an example for other areas where incorporating a cooperative approach could positively influence bobwhite populations.

Citation: Peters, G. M., M. W. Hook, M. S. Garner, J. M. Margniez, C. W. McKinney, and J. S. Nanney. 2017. Partnering for quail in South Carolina: a cooperative approach making a difference. National Quail Symposium Proceedings 8:149.

Key words: *Colinus virginianus*, collaboration, habitat restoration, Indian Creek, northern bobwhite, partnerships, savanna, woodland

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CONNECTING LAND ETHICS AND ENTREPRENEURSHIP THROUGH EXPERIENTIAL LEARNING IN A BOBWHITE CENTRIC OUTDOOR EDUCATION PROGRAM

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ABSTRACT

The majority of today's youth have the ability to utilize consumer technology on a regular basis. This access has exacerbated the disconnect between adolescents and the natural environment by reducing the amount of time spent outdoors. To compound this disconnect, the continued use of traditional classroom settings along with the "sit-and-get" style of facilitation, widens the gap between inert knowledge and applied knowledge. The transformation from theory to practice witnessed in outdoor science, technology, engineering and mathematics (STEM) education has been shown to foster the assimilation and retention of STEM concepts. Therefore, educational institutions have begun to cultivate the implementation of experiential learning programs in order to provide the appropriate setting for students to establish relationships between theory and application. This study investigated the relationship between experiential learning and content information retention in a bobwhite centric outdoor education program in which participants were given the task of creating a habitat management plan for a tract of land by utilizing entrepreneurship skills acquired over the course of camp. The study participants consisted of north Texas youth and program facilitators. Pre- and post-assessments were administered on the first and last day of the program. The data indicate an increase in content information retention among participants in experiential settings. The results are consistent with similar studies that have analyzed experiential learning methodologies and their impact on data retention. We recommend that the experiential approach be further applied and tested in youth outdoor education programs.

Citation: Bowling, G. M., A. P. Tynes, and K. S. Reyna. 2017. Connecting land ethics and entrepreneurship through experiential learning in a bobwhite centric outdoor education program. National Quail Symposium Proceedings 8:150.

Key words: quail, entrepreneurship, experiential learning, land ethics, outdoor education program, STEM education

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CONTRIBUTIONS OF TRANSLOCATION TO NORTHERN BOBWHITE POPULATION RECOVERY

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ABSTRACT

The National Bobwhite Conservation Initiative (NBCI 2.0) is a range-wide plan for recovering northern bobwhites (*Colinus virginianus;* hereafter, bobwhite[s]). Using geospatial analysis informed by expertise from practitioners, the plan categorizes landscapes into restoration potential by weighing biological constraints and opportunities such that targeted habitat management will produce bobwhite population growth. A fundamental assumption of the NBCI 2.0 for achieving recovery goals is that bobwhite source populations currently exist on the landscape at densities necessary to (re)colonize newly established or improved habitat. However, we have found that these source populations can be very low or non-existent, especially in northern tiers of the bobwhite distribution. In 1997, we initiated research to evaluate bobwhite population response following translocation using birds from high density populations to newly developed habitats with low bobwhite numbers (<1 bird per 0.62 ha). We worked collaboratively with the Georgia Department of Natural Resources in 2006 to develop and implement a wild bobwhite translocation policy based on key findings from that research. Since that time 3,866 wild bobwhites have been trapped and translocated from properties in the Albany and Greater Red Hills region of Florida and Georgia to 13 recipient sites in 6 states (AL, GA, MD, NC, NJ, and SC) on 29,780 ha. A typical translocation was conducted for 2 – 3 years in March by capturing, tagging and transporting birds overnight for release at an average rate of 1 bird per 7 ha per property. Prior to translocation, each recipient property underwent extensive habitat restoration and agreed to conduct a monitoring program including spring whistle counts and fall covey counts before, during, and after translocation. Bobwhite populations increased on recipient sites from an average of 0.38 (CI: 0.13 – 0.63) birds per hectare to 2.2 (CI: 1.45 – 2.95) birds per hectare resulting in the establishment of huntable wild bobwhite populations adding approximately 42,714 bobwhites to the landscape. The value of these wild bobwhites was determined to average $736 per translocated bird bringing the total value of birds donated from the Albany and Greater Red Hills region for translocation to $2,844,564. The establishment of population hubs through translocation contributes to population recovery efforts outlined in the NBCI 2.0, especially where source populations are limited.

Citation: Sisson, D. C., T. M. Terhune II, W. E. Palmer, and R. E. Thackston. 2017. Contributions of translocation to northern bobwhite population recovery. National Quail Symposium Proceedings 8:151–159.

Key words: *Colinus virginianus,* Florida, Georgia, habitat, National Bobwhite Conservation Initiative, NBCI 2.0

INTRODUCTION

The National Bobwhite Conservation Initiative (NBCI 2.0) encourages intentional habitat management to benefit northern bobwhites (*Colinus virginianus*; hereafter, bobwhite[s]) and grassland and/or shrub obligates. Specifically, the call to maintain management on existing areas with wild bobwhite, development of new areas managed for wild bobwhite, and the establishment of habitat epicenters to facilitate population recovery was identified in the national plan as precursors to success (Palmer 2011). The widespread decline of bobwhites has resulted in local, and in some cases regional, extirpation of bobwhites (Brennan 1991) yet where quality habitat exists at a scale suitable for long-term sustainability bobwhite populations have remained stable to increasing (Brennan 1991, Terhune et al. 2007, Stribling and Sisson 2009). Smaller habitat patches and more isolated bobwhite populations are not only more prevalent in today's landscape but are much more vulnerable to extirpation due to stochastic events (e.g., weather), especially in northern tiers of their distribution (Janke

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and Gates 2012, Janke et al. 2015). Therefore, restorative habitat management may not result in short-term increases in bird abundance, if at all, especially where the landscape lacks consistent source populations of bobwhites. In these cases, habitat management alone may not result in bobwhite population recovery.

Translocation as a tool to restore or augment current bobwhite populations has been successfully applied to contiguous and fragmented sites in the Southeast (Terhune 2008, Terhune et al. 2005, 2006 and 2010). Despite these successes, some still question the reliability of the technique alone for broad-scale population recovery (Brennan 2012). Terhune et al. (2010) emphasized that translocation was not a substitute to management and highlighted that careful site selection and habitat management were precursors to its success. As such, high density bobwhite populations serve as source populations for translocation and may provide an opportunity to develop new population hubs for restoring bobwhites where habitat exists at sufficient quality and scale and where birds have been extirpated due to inclement winter weather (Palmer et al. 2011, Janke et al. 2015).

To date, the cost of wild quail management and translocation has also not been well documented. The estimated annual economic impact of working lands in the Red Hills and Albany regions are $147.1 million and $125 million, respectively (Fleckenstein 2013 and 2014). The Center for Economic Forecasting and Analysis at Florida State University additionally estimates that $115 million and $82 million, respectively, is a direct result of expenses associated with intensively managed quail lands (Fleckenstein 2013 and 2014). These impacts reflect annual operating expenses, capital improvement expenses, discretionary spending, and charitable giving, but proportional expenses attributed directly to the production of wild bobwhites is currently lacking. Given that the annual expenses reported in Fleckenstein (2013 and 2014) are beyond that required to maintain a population of wild bobwhites and would over-estimate the value of a wild bobwhite, we collected annual budget information for private properties in the Red Hills and Albany Area to determine annual costs associated specifically with bobwhite habitat management. Additional costs were evaluated as well to determine the total value of trap and translocated wild quail.

The history of wild bobwhite translocation and development of Georgia's translocation policy was summarized in Sisson et al. (2012). At that time the implementation phase of these projects had just begun with a total of 945 birds translocated onto 8,860 ha. Since that time, significant progress has been made with this program as it was expanded in both size and scope. As a result of preliminary findings and more recent successes, widespread interest in the utility of translocation as a conservation tool has gained traction. But, the overall contribution and cost of translocation to population recovery efforts has not been documented. Brennan et al. (2012) pointed out the glaring omission of success stories in previous National Quail Symposiums and called for an increased effort at publishing them, as this would be how the success of NBCI 2.0 would be judged. Herein, we describe the contributions made towards the NBCI 2.0 wild bobwhite recovery goals by the wild quail translocation program being conducted by Tall Timbers Research Station's Game Bird Program and our partners.

STUDY AREA

Donor sites for this effort were all privately owned wild quail properties in the "Plantation Belt" of southwest Georgia and north Florida in the vicinity of Albany and Thomasville, GA and Tallahassee, FL (Figure 1). Two of these properties, Tall Timbers and Dixie Plantation, are owned and operated by Tall Timbers Research Station and Land Conservancy (TTRS). All donor properties have a long history of wild quail management and hunting, maintaining high density ($>$2.5 birds per ha) wild bobwhite populations (Brennan et al. 2006, Sisson et al. 2012), with many of these populations supporting $>$1 (range: 0.42 – 8.65) birds per hectare on these sites. There have been 13 recipient sites to date in 6 states (AL, GA, MD, NC, NJ, and SC) ranging in size from 600 to 5,600 ha (Table 2 & Figure 1). Recipient sites were all large ($>$600 ha), privately-owned properties that are comprised predominantly of open pine (*Pinus* spp.) timber with integrated wildlife openings. These recipient sites have all undergone habitat modification/improvement before translocation was conducted and operate under a long-term management plan incorporating regular prescribed fire ($<$3 year fire-return interval), low-density timber (10 – 65 BA with an average of 35-40 BA) and wildlife openings incorporating fallow field management and/or crop rotations. In addition, post-burn mowing or roller chopping is commonly applied to reduce mid-story hardwood encroachment as well as reduction of mature hardwoods in upland sites. Many of these properties also implement year-round supplemental feeding and year-round mammalian predator control to maintain targeted ($<$15% predator index) predator activity levels. The predator index is calculated as the proportion of scent stations hit by target mammalian meso-predators. During translocation, quail hunting is precluded from these recipient sites to allow for maximum over-winter survival and carryover to breeding season for optimal reproduction in subsequent years.

METHODS

Translocation

Translocation was conducted between 2003-2016 in every year but 2005, and occurred in March following the protocol outlined in Terhune et al. (2005, 2006, 2010) where birds were captured using baited funnel traps (Stoddard 1931) held and/or transported overnight, and released at the recipient site the following day. Each bird was leg banded, weighed, and classified by sex and age. Some projects included a research component involving radio telemetry in which a sample of birds were radio-tagged with 6g necklace style radio-transmitters (Holohil Systems, Carp, Ontario, Canada). All trapping and

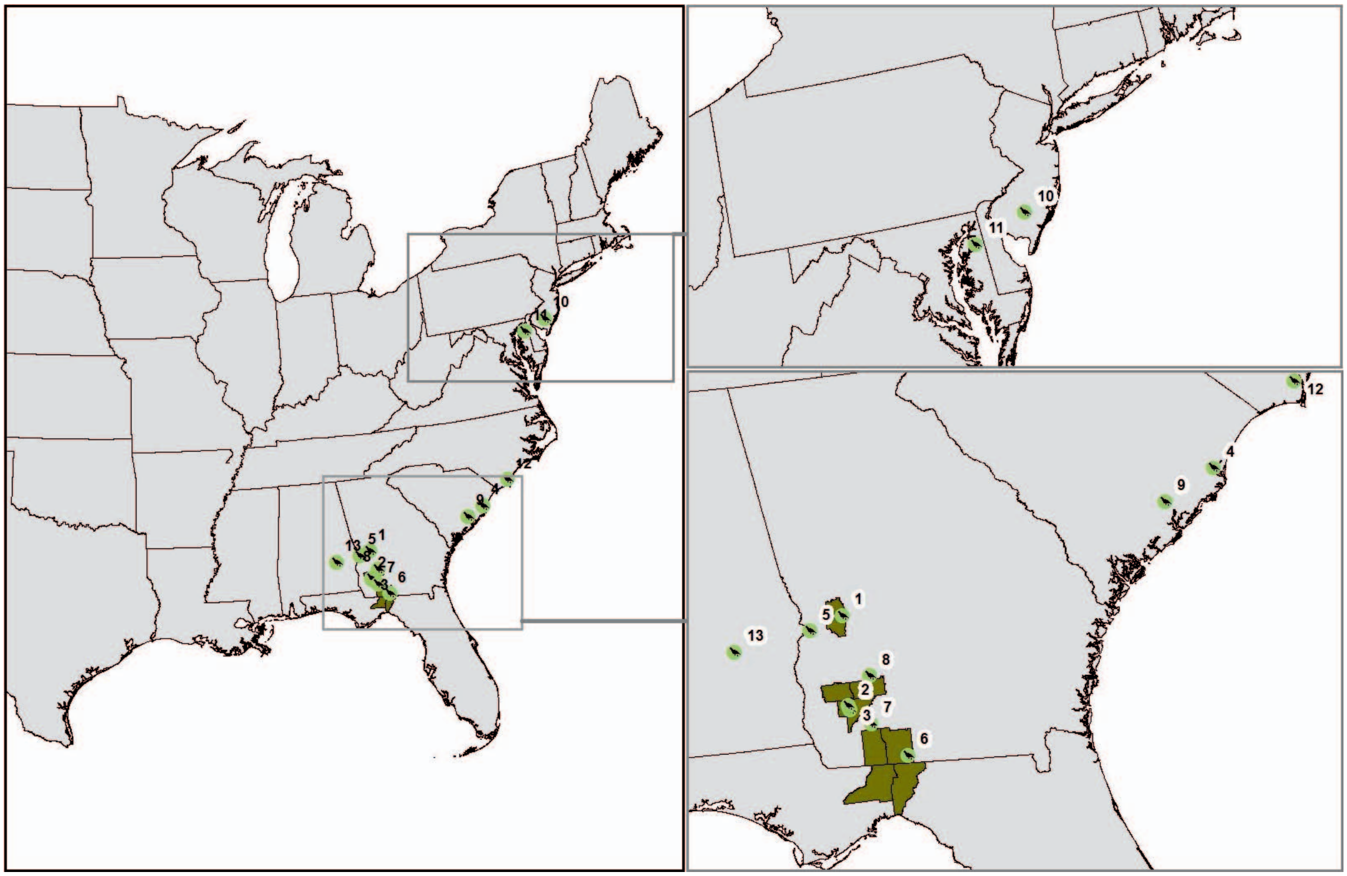

Fig. 1. General location of sites in south Georgia and north Florida (green shaded counties) that donated 3,866 wild northern bobwhites for translocation between 2003-2016 as well as location of 13 sites (indicated by bobwhite icons and labelled as site numbers 1 – 13) receiving the translocated birds in 6 states.

handling procedures were approved by either Auburn University's (2002-2007: AU-2002-0364) or Tall Timbers Institutional Animal Care and Use Committee (IACUC numbers: TTRS, GB-2001-01 and GB-2001-01-15) and permitted by either the Georgia Department of Natural Resources, Wildlife Resources Division (GA DNR WRD) or the Florida Wildlife Commission (FWC). Personnel from TTRS Game Bird Program served as the "agent" for each translocation.

Monitoring

Bobwhite populations were monitored at all translocation sites prior to, during, and after translocation using spring whistle counts and fall covey point counts (both assuming a 500-m detection radius) as an index to population change over time. Spring whistle counts followed the standard protocol developed by Terhune et al. (2009) which was based on previous research (Curtis et al. 1989, Ellis et al. 1969, Hanson and Guthery 2001, Rosene 1969, Wells and Sexon 1982) where a series of points was visited by an observer recording individual males heard for five minutes during the first two hours after sunrise. The number of points for each property varied with the size of the property whereby a minimum of 20% of the total area was targeted for sampling and systematically stratified across the property to ensure adequate spatial coverage. We ascertained the peak calling week by calculating the average number of individual calling males at all points for each study site. We conducted weekly counts during the first peak of calling activity (late May – early June) which has been shown to correlate well ($R^2 = .975$) with autumn abundance on our study areas in south Georgia and north Florida (Terhune et al. 2009). We used covey call indices (DeMaso et al. 1992, Seiler et al. 2002, Wellendorf et al. 2004) from mid-October to late November and estimated abundance using the point count method via the fixed radius approach adjusted for calling rate based on factors outlined in Wellendorf et al. 2004 (e.g., wind speed, barometric pressure, and adjacent calling coveys). Upon determining the adjusted number of coveys per point, we used a multiplier for the number of birds in a covey to calculate the total number of birds in a sampling area and divided that number by the size of the area sampled (78.5 ha*number of points) to obtain the bird density (birds per hectare) for a given property. The average covey size was determined by using pointing dogs during fall census as well as flushing of radio-tagged coveys on sites when available. The point counts conduced in the fall were the same points as the spring whistle counts and repeated 2 times. Whistle counts were used as a measure of trends in the population over time while covey counts gave a measure of autumn density (birds per hectare) and were

Table 1. Average annual costs (on a per acre basis) for typical northern bobwhite land management activities in the southeastern United States

Budget Item	Included in Estimation of Value per Bird	CPA[a]	SD[b]
Salaries/Payroll	Yes	$32.47	$12.82
Payroll Benefits/Taxes	Yes	$12.68	$5.51
Vehicles	Yes	$1.19	$0.76
Woods Management / Land Clearing / Forestry [c]	Yes	$19.62	$6.34
Quail Management & Development [d]	Yes	$7.43	$3.57
Contract Services [e]	Yes	$5.17	$4.21
Equipment Purchase/ Lease [f]	Yes	$5.49	$4.76
Equipment Maintenance/ Repairs	Yes	$4.95	$3.43
Fuel & Travel	Yes	$4.96	$1.85
SubTotal		$93.96	$25.31
Other Expenses			
Buildings/Ground Maintenance	No	$7.31	$3.29
Utilities	No	$4.62	$2.12
Property Tax & Insurance	No	$5.81	$5.59
Dog Program	No	$3.52	$3.42
Horse Program	No	$2.82	$2.74
Miscellaneous	No	$0.90	$0.59
Recreation	No	$2.52	$2.74
Depreciation/Amortization	No	$6.44	$3.69
SubTotal		$33.94	$24.19
Total		$127.90	$41.23

[a] Cost per acre.

[b] Standard deviation.

[c] Land clearing includes snag cleanup, hardwood reduction, pile management, and etc.

[d] Quail Management and development includes prescribed burning, fallow field creation and maintenance, supplemental feeding, predation control, and etc.

[e] Contract services include prescribed burning, chemical (herbicide) purchase and application

[f] Equipment Purchase or lease includes purchase of new equipment such as tractors, ATVs and land management implements (e.g., mowers, harrow/disk, roller chopper, spreader, etc.) or lease of equipment such as tractors, front-end loaders, excavators.

used to calculate the number of birds produced over time by the translocation and management efforts.

Estimating Value per Bird

We collected annual budget information for private properties (n = 17) in the Red Hills and Albany Area to determine annual costs associated specifically with bobwhite habitat management. We identified expenses directly associated with land management activities and calculated the average cost per acre managed for each budget item category available for each property and excluded those budget items not directly associated with land management activities such as property taxes and insurance, housing maintenance and utilities, bird dog programs, horse programs, and general recreation (see Table 1). We ascribed the value of an individual wild bobwhite in the Red Hills and Albany region by estimating annual operating cost associated with the production and maintenance of a wild populations with the underlying assumption that a translocated bird is equivalent to a harvested bird when harvest is considered compensatory and not additive. This was considered a conservative, "best case" scenario but may not apply to all sites and regions. Thus, we estimated the value of a translocated wild bobwhite (VB) as:

$$VB = MC + OC + TTC$$

where, MC is the cost associated with land management, OC is the opportunity cost, and TTC is the trap and transport cost associated with translocation. Subtracting TTC would then provide the value of a wild bobwhite in the Red Hills and Albany area. We calculated the management cost as:

$$MC = \left(\frac{Annual\ Land\ Management\ Budget}{FA^{*}HR^{*}WA}\right)$$

where, the annual land management budget includes only those land management activities directly associated with the management of bobwhites, FA (fall abundance) is the estimated total number of birds on a property during the October/November fall census, HR is the harvest rate of 0.15 which reflects the recommended harvest rate to maintain long-term population persistence in the Southeast, and WA is winter attrition due to natural predation. A 15% harvest rate is recommended (W.E. Palmer, unpublished data) to mitigate potential additive take of bobwhites during any given hunting season, and the number of translocated birds donated plus the total birds harvested should not exceed this 15% recommended harvest rate to preclude any additive harvest effects. In our study, since all donor properties stayed at or below the 15% recommended harvest rate including birds removed for translocation purposes, WA was 1 (i.e., no effect) since translocation was considered compensatory in our populations. However, in populations where harvest is considered additive we suggest WA should reflect that the value of a bird in mid-March which is higher than in mid-October such that WA would be calculated as:

$$WA = DSR^{\#days}$$

where, DSR is the mean daily survival rate and # days represents the number of days passed since the timing of the fall census. For example, on our sites in the Southeast average DSR during the fall/winter time period is 0.9975 and 135 days pass from the time of our fall census and the start of translocation suggesting that survival during that period is 0.56 (or 56% of

Table 2. Site number, recipient location (county), size, years conducted, number of translocated birds, pre- and post-translocation density, and birds added to the landscape on sites receiving wild northern bobwhite translocations from South Georgia and north Florida conducted by Tall Timbers Game Bird program from 2003-2016.

							Density (birds per ha)		
Site #	County	State	Size (ha)	Distance (km)	Years	# Birds	Pre	Post	# Birds Added
1	Marion	GA	1,200	116	2003-2004	127	0.75	3.25	3,000
2	Baker	GA	800	16	2006	100	0.50	1.25	600
3	Baker	GA	720	13	2007-2009	219	0.35	1.56	871
4	Georgetown	SC	2,200	687	2009-2011	401	0.38	3.50	6,864
5	Stewart	GA	1,920	115	2011-2013	524	0.08	2.38	4,416
6	Thomas	GA	1,000	28	2011	60	NA	NA	NA
7	Mitchell	GA	600	21	2012-2013	105	0.13	1.00	525
8	Lee	GA	3,360	43	2012-2014	327	0.38	3.00	8,820
9	Berkeley	SC	3,600	470	2013-2016	451	0.38	1.88	5,418
10	Burlington	NJ	5,600	1,292	2015-2016	164	NA	NA	NA
11	Kent	MD	2,700	1,207	2015-2016	128	NA	NA	NA
12	Brunswick[a]	NC	4,480	680	2013-2017	1,058	0.25	2.75	11,200
13	Bullock[a]	AL	1,600	170	2015-2017	202	0.63	1.20	1,000
Total			29,780			3,866			42,714

[a] Translocation still in progress through 2017

[b] Bobwhite density (birds per hectare) was calculated by using point counts following Wellendorf et al. 2004 to obtain an adjusted number of coveys (corrected for factors influencing calling rate), multiplied by the average covey size observed per site, and divided by the total area sampled (78.5 ha * number of points).

[c] NA values indicate data that was unavailable due to monitoring constraints during some years on some sites.

bobwhites alive during mid-October remain alive during mid-March; see Terhune et al. 2007).

The opportunity cost (on a per bird basis) was calculated as:

$$OC = \left(\frac{Cost\ of\ a\ Wild\ Bobwhite\ Hunt}{Daily\ Bag\ Limit}\right) - MC$$

where, the average current cost of a wild quail hunt (~$7000 per day) and the daily bag limit for the hunt (24 quail for a 2-person wagon limit). We calculated the cost associated with trap and transport for each translocation conducted since 2003, where data was available, as:

$$TTC = \frac{(PT + TP + PB + Trap + Transport + Misc)}{\#birds}$$

where, PT is personnel time required for all activities associated with trapping (pre-baiting, running traps, working up birds, and travel); TP is the expense associated with permitting and health screening (extracting blood samples or mouth swab for disease testing); PB is costs incurred relative to pre-baiting including truck mileage, fuel, and bait; Trap is the cost incurred from running traps which includes trap materials, truck mileage, fuel, and bait; Transport is the cost associated with transporting of birds from the source sites to the recipient site including truck mileage and fuel; Misc includes miscellaneous charges associated with translocation (overnight stays during transport of birds, shipping of bird samples for health screening, etc.); and, # birds represents the total number of birds captured and moved during a translocation.

RESULTS

During 2003-2016 we translocated 3,866 wild bobwhites from donor sites in southwest Georgia and north Florida to 13 recipient sites in 6 states (AL, GA, MD, NC, NJ, and SC). Twelve anonymous, private donor sites in addition to the 2 sites owned by TTRS contributed birds for translocations with care taken in each case to distribute the birds removed among properties so as not to harm the resident populations and adhere to the maximum 15% recommended harvest rate. The typical translocation was for 3 consecutive years and averaged 1 bird released for every 7 ha on the recipient site. The average recipient site (property) size was 2,290 ha with an overall (all sites) combined 29,780 ha of new centers created for wild quail populations. Fall densities on these sites increased from an average of 0.38 (CI: 0.13 – 0.63) birds per hectare to 2.2 (CI: 1.45 – 2.95) birds per hectare (Table 2). We estimated this added 42,714 birds to the landscape, with several of these populations still growing. Population recovery on some sites was dramatic as indicated by both whistle counts and fall covey counts. For example, on the site in Lee County, Georgia only 120 males and 15 coveys total were heard from 9 listening points in the year prior to translocation beginning. Four years later, these numbers had increased to 20 males and 90 coveys heard (Figure 2). This equated to a population increase in fall density from 0.38 birds/ha (CI: 0.16 – 0.65) prior to translocation in 2011 to 3.0 birds/ha (CI: 2.14 – 3.86) in 2015 (Table 2). Similarly, on the site in Brunswick County, North Carolina the spring whistle and fall covey counts increased from a total of 5 males and 10 coveys heard on 20 points initially to 97 males and 114 coveys four years later (Figure 3).

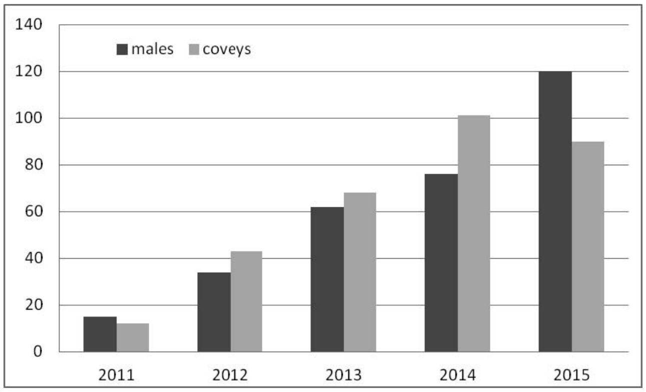

Fig. 2. Total number of whistling males in spring and autumn coveys heard from 9 listening points on a 3,360 ha translocation site in Lee County, GA before (2011), during (2012-2014), and after the translocation of 327 wild northern bobwhites.

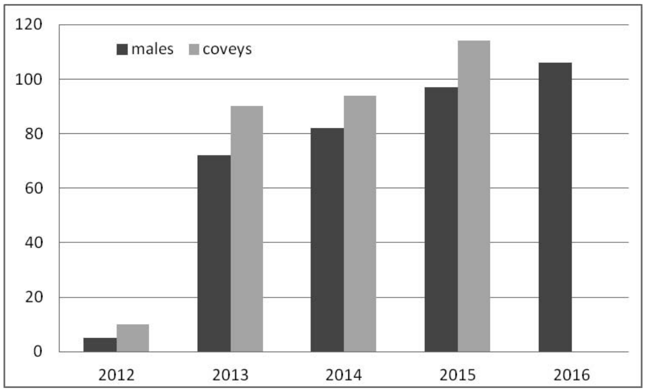

Fig. 3. Total number of whistling males in spring and autumn coveys heard from 20 listening points on a 4,480 ha translocation site in Brunswick County, NC before (2012) and during (2013-2016) the translocation of 1,058 wild northern bobwhites.

The estimated annual management cost associated with bobwhite habitat management was \$93.96 (± 25.31) per acre (Table 1). We found that on average the management cost (MC) was \$398.63 (± 181.33) per bird, opportunity cost (OC) was \$170.92 (± 107.48) per bird, trap and transport cost was \$166.24 (± 65.71) indicating that the total value of a translocated wild bobwhite was \$735.79 (± 267.79). We found that as bird density on source sites increased, OC increases whereas MC decreases and TTC also cost decreases. If this value is applied to all birds donated for translocation (n = 3,866) the total value of birds donated was \$2,844,564.

DISCUSSION

Our results suggest that when translocation is implemented following habitat restoration and/or concurrently with sound habitat management, population growth is expected. However, given our study design (i.e., lack of a true control due to property size constraints) it is difficult to attribute the magnitude of population response exclusively to translocation because improved habitat management occurred simultaneously. Intentional habitat management occurred all our study sites and, in fact, was a pre-requisite for translocation in all cases because previous research has demonstrated the necessity of habitat management for demographic success following release (Terhune 2008, Terhune et al 2005, 2006, 2010). However, it is important to note that these population increases occurred against a backdrop of long-term regional population declines (Sauer et al. 2015), and the extent of population growth on translocation sites ($\bar{x}=$ 182% increase ± 55.6%) was much times greater compared the managed sites ($\bar{x}=$ 6.9% increase ± 6.4%) not receiving translocation in the Red Hills and Albany areas (see Figure 4). Thus, the numerical benefit of translocation on bobwhite abundance may serve as an added boost to habitat management. Furthermore, this habitat work may not have occurred without the assurance of translocation as an option.

While some of the early research on translocation provided mixed results (Jones 1999, Liu et al. 2002), we remained optimistic since our results in South Georgia demonstrated time and again that translocation worked under proper conditions (Terhune et al. 2005, 2006, 2010). The development of the GA DNR WRD program in 2006, and preliminary results, further bolstered our confidence (Sisson et al. 2012) as well as created a great deal of interest in the program from landowners and other state wildlife agency programs. This is evidenced by the fact that in the first 10 years of the program 8 translocation projects were initiated moving a total of 945 birds, compared to the last 4 years when another 5 projects have been initiated resulting in over 2,000 birds moved. The success of this program has to be considered more than marginally significant as it has contributed to the addition of approximately 42,714 birds to the landscape and helped create 29,780 ha of new wild bobwhite population centers in six states. In our studies, we could not fully infer how genetic differences among source and recipient sites influence the success of translocation since nearly all of our translocations occurred in the Southeast. Previous research has shown that the role of genetics, through ostensible hybrid vigor, genetic swapping or increased heterozygosity, does not likely explain population growth following translocation (Terhune 2008). However, future research should explore how phenotypic traits such as body size and other genotypic expressions such as behavior or habitat selection might influence the success of translocation across greater latitudinal or longitudinal distances.

The need for translocation as a population recovery tool is increasing as evidenced by range-wide population declines, local/regional extirpations (Sauer et al. 2015) and the low initial population densities (<1 bird per 0.62 ha) on some of our study sites even following extensive habitat management (Stribling and Sisson 2009, Sisson et al. 2012). While the average density on our recipient sites was low (0.38 birds/ha) some were as low as 0.08 birds/ha, much lower than what is considered a huntable population (Palmer et al. 2011). Some northern states have closed bobwhite hunting season altogether and have

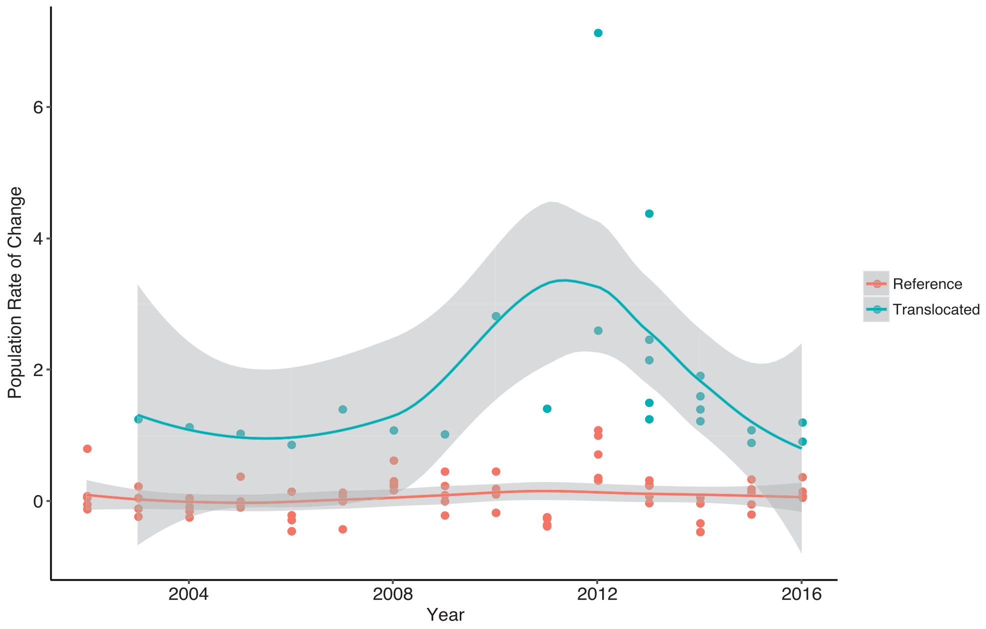

Fig. 4. Northern bobwhite population growth, represented as rate of change from fall to fall, for translocated sites compared to reference sites (n = 5) during 2001 - 2016.

reported no wild bobwhites remaining in some areas or the entire state (see NJ Fish and Wildlife 2015). The possibility of translocation to supplement birds and jumpstart population recovery provides landowners added confidence to move forward with a wild bobwhite management program. While populations on many of our study sites would have likely increased on their own, it may not have been fast enough for these landowners to justify the expense or for the bobwhite population to overcome barriers (e.g., stochastic weather events, lack of conspecifics) to population growth. We believe that individual state translocation protocols are necessary to provide the framework for translocation and set side-boards for minimum criteria required for qualifying as a recipient site. In doing so, the protection of a limited source of birds also indemnifies those landowners contributing birds to the cause.

In the early to mid-1900s bobwhites were byproducts of everyday land use, but today intentional and purposeful management is required to maintain wild bobwhite which can be an expensive proposition, especially in the Southeast (Burger et al. 1999, Palmer et al. 2011). The intensity of management and cost is high in the Southeast and is unparalleled anywhere in the bobwhite distribution. A conservative harvest (<15% of the fall population) is part of the management philosophy and a contributing factor to their long-term success (Sisson et al. 2012), but it also makes the value per harvested bird high. Other studies have shown the value per harvested quail to range from $254 on a lease in Texas (Johnson et al. 2012) to over $300 per bird on a state Wildlife Management Area in Georgia (GA DNR WRD unpublished data) which does not include opportunity cost since commercial hunts are not an option on public lands. We found that the value per harvested wild bobwhite to be $570 per bird and the value of a wild translocated bird to be $736 per bird which may be on the low end of the scale for private plantation properties. At this rate the value of the 3,866 birds contributed to the translocation program was $2,844,564 which underscores the conservation ethic of donor site owners. Not only are these landowners making significant contributions to bobwhite conservation by maintaining stable bobwhite numbers and contributing birds to population recovery efforts, but they also are provide a major boost to local economies – estimated in the millions annually (Fleckenstein 2013 and 2014). The NBCI 2.0 recognized the importance of existing high density populations as sources for both population expansion and translocation (Palmer et al. 2011). Approximately 280,000 ha of private land in Albany and Greater Red Hills region is actively managed for bobwhites. The contribution of these landowners and their staff to quail conservation, the local economy, and now on a regional and even national scale as donors for translocation is laudable. The collective contribution of translocation to population recovery is significant and stems from a dedicated partnership between Tall Timbers, state wildlife agencies, and private landowners. The success of this translocation program underscores the value of partnerships to bobwhite population recovery and wildlife conservation as a whole. Given the limited commodity of wild bobwhites and their socio-economic value, we have a responsibility to judiciously implement translocation with the utmost care and careful consideration of science-based recommendations.

We believe our continued success of translocation is due to strictly following recommendations from past research. Specifically, we view five primary criteria contribute to the success of translocation: (1) large target release area; (2) quality habitat and continued management on the release site; (3) an available source of wild bobwhites; (4) short capture, handling, and holding times;

and, (5) timing of release. Given adequate habitat management and a valid source of wild bobwhites, we also recommend translocating individuals 3–4 weeks prior (during mid-to-late March) to the breeding season to provide ample acclimation time to their new surroundings, but not longer than 3–4 weeks prior to breeding season to reduce potential mortality (see Terhune et al. 2005, 2006, 2010). We recommend (based on movement and dispersal data from previous research – see Terhune et al. 2005, 2010) that release sites should be as large as possible, but minimally should be at least 600 ha to reduce dispersal outside managed habitat. Our experience also has been that survival, subsequent reproduction, and population growth can be suppressed on a property with a prior history of pen-reared releases (D.C. Sisson, unpublished data). As such, we suggest waiting 2-3 years following any release of pen-reared birds prior to implementing translocation on a property. In addition, we believe that birds should be released as soon as possible and not held in captivity for more than 24 hours to reduce stress associated with capture, handling and holding. Future research on identifying proper stocking rate (number of birds released), spatial distribution of releases relative to conspecific presence, soft versus hard releases, and temporal replication necessary to elicit a desired population response is warranted to maximize the efficacy of translocation.

MANAGEMENT IMPLICATIONS

The population growth we observed on all properties demonstrated by this wild bobwhite translocation program contributes directly and significantly to the population recovery goals outlined in NBCI 2.0. The partnership between private landowners, state wildlife agencies, and NGOs could serve as a model for similar programs in other areas. Creation of new population hubs through focused and intentional habitat management may serve as source populations for either local expansion or additional translocations improving the overall likelihood for population recovery of northern bobwhites. Local economic impacts to rural areas along with instilling confidence in landowners and managers on private and public lands wishing to attempt restoration efforts is value added to bobwhite conservation. Lastly, we submit that future translocations should carefully consider previous research and recommendations on maintaining (1) large target release area(s); (2) quality habitat and continued management on the release site(s); (3) holding and transport times; and, (4) proper timing of release to increase the probability and level of success warranted by a species of high socio-economic value and a limited resource.

ACKNOWLEDGMENTS

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EXPERIENCES IN NORTHERN BOBWHITE PROPAGATION AND TRANSLOCATION IN OHIO, 1978–2012

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ABSTRACT

Ohio once boasted a population of 7 million northern bobwhites (*Colinus virginianus*). Catastrophic blizzards during 1976–1977 and 1977–1978 brought winter quail mortalities of 85% and 80%, respectively. Ohio's bobwhite population was 430,000 in 1978, a 90% reduction from 1976. Remnant quail populations were small, isolated, and incapable of rapid recovery. The Ohio Department of Natural Resources (ODNR) initiated a statewide stocking effort to expedite population growth. The ODNR chose to propagate wild quail in captivity and release first-generation progeny (F1). Throughout 1980–1986, the ODNR released 65,000 F1 quail statewide. The ODNR monitored population response with North American Breeding Bird Survey, mail carriers, and roadside whistle-counts, but found little evidence of success. The ODNR evaluated postrelease survival and productivity of F1 hens ($n = 100$) and wild hens ($n = 40$) during 1984–1986 and deemed F1 hens inferior to wild hens. In 1993, the ODNR produced population models to develop minimum stocking rates for wild quail translocation, but insufficient numbers were captured. From 1998 to 2000 and 2005 to 2009, the ODNR translocated wild quail from Kansas to 5 Ohio sites with suitable, unoccupied habitat. Concurrently the ODNR translocated wild quail within Ohio. The ODNR conducted annual spring whistle-counts on all release sites during 1998–2012. Little or no evidence of sustained populations existed on sites after 7 years. Bobwhite translocation may yet show promise for population restoration, but evaluation should include 7–10 years of monitoring at a minimum.

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During 1960–1976, autumn populations of northern bobwhite (*Colinus virginianus;* hereafter, bobwhite) in Ohio averaged >4.5 million birds and occupied all 88 counties in the state. Annual fluctuations of up to 40% from this population mean were considered normal during this time (Urban 1978). Bobwhite populations in Ohio and other states along the northern extent of the range are subject to temporary, precipitous depressions as a result of periodic severe winter weather events (e.g., blizzards). For example, statewide bobwhite populations declined to a fraction of their previous level during the winters of 1935–1936 and 1944–1945. In the years following these events, more favorable weather prevailed and populations rebounded with little or no assistance from wildlife managers (Dambach 1948).

Ohio bobwhite populations reached unprecedented lows following catastrophic blizzards in the late 1970s (Sauer et al. 2014). The Ohio Department of Natural Resources (ODNR) recorded abnormally high bobwhite mortality (85% and 80%, respectively) during the winters of 1976–1977 and 1977–1978. Losses were thought to be most severe in the northern half of the state, where bobwhites were believed to have been extirpated within some counties. In addition, spring to autumn increases in 1977 and 1978 (58% and 166%, respectively) were well below the documented average (294%; Urban 1978). Urban (1978) attributed these unusually low reproduction rates to the poor body condition of bobwhites in the spring following extremely severe winters. In 1978 Ohio's autumn bobwhite population was estimated to be 430,000, >90% below the 17-year mean (Urban 1978). The ODNR closed the bobwhite hunting season statewide in 1978 and began to consider strategies to expedite population recovery.

Prior to 1976, the ODNR considered artificial propagation and translocation to be ineffective and unnecessary management actions for bobwhite. Any potential benefit derived from these activities was likely incidental to natural production (Dambach 1948). In addition, all available habitat within the state was thought to be occupied at the time, leaving little potential to expand the range or increase abundance of bobwhite in Ohio (Ohio Division of Wildlife 1955). By 1978, the ODNR believed large amounts of suitable habitat were unoccupied in the state, including several counties with extirpated bobwhite populations. The ODNR believed sufficient habitat existed in 1978 to support bobwhite populations at or near levels observed statewide in 1976, yet acknowledged the possibility that the state's remnant

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bobwhite population did not possess the capacity to return to preblizzard abundance and distribution without assistance (Urban 1978).

The ODNR made numerous efforts to reestablish bobwhites in the state through propagation and translocation during the past 3 decades. Unfortunately, populations remain at near-record lows, and the bobwhite range in the state appears to be contracting (Spinola and Gates 2008). Interest in captive propagation and wild translocation persists, particularly in areas outside the remnant bobwhite range in the state. Within this paper we have prepared a summary of the ODNR's bobwhite propagation and translocation projects since 1978, and we offer some interpretation of project results. This information should provide insight into some problems associated with bobwhite propagation and translocation efforts, and encourage investigation of unanswered questions.

METHODS

We conducted a comprehensive review of published and unpublished information on bobwhite propagation and translocation attempts conducted by the ODNR during 1978–2012. We amassed and summarized all relevant information including research reports, project updates, and miscellaneous interagency documents.

RESULTS

The ODNR's efforts to restore statewide quail populations in Ohio were continuous throughout 1978–2012, but methodology evolved as the ODNR identified and altered ineffective techniques. We distinguish between 2 distinct projects implemented by the ODNR, including 1) captive propagation of wild-caught bobwhite, and 2) translocation of wild-caught bobwhite.

Captive Propagation

During the winter of 1978, ODNR staff captured wild adult bobwhites using baited funnel traps and transported them to the state-owned Wildlife Propagation Unit in Urbana, Ohio. The ODNR captured 379 wild bobwhites during the winter of 1978 and supplemented this breeding population with an unknown number of wild birds captured in subsequent years (S. Norris, ODNR, personal communication). Wild-caught bobwhites were paired within indoor 5-row battery breeding cages and egg laying was artificially stimulated using lights. Eggs collected from breeding cages were placed in an incubator until hatching occurred. Newly hatched first-generation (F1) chicks were kept in heated brooder pens for 3–4 weeks before being allowed outside. At 10–14 weeks the F1 bobwhites were moved to 45.5-m-long outdoor, wire-floored, flight conditioning pens. Flight conditioning pens promoted acclimation to the elements and were large enough to allow birds to exercise legs and wings. Vegetation cover within the flight pens consisted of evergreen boughs and herbaceous weeds growing through the wire floor. Chicks were fed 28% protein poultry starter for 2 weeks, followed by 26% protein feed until 8 weeks, and then 20% protein poultry pellets until release. Most food and water was provisioned automatically, and human contact was minimized. Antibiotics were administered as normal practice (Henry and Shipley 1989).

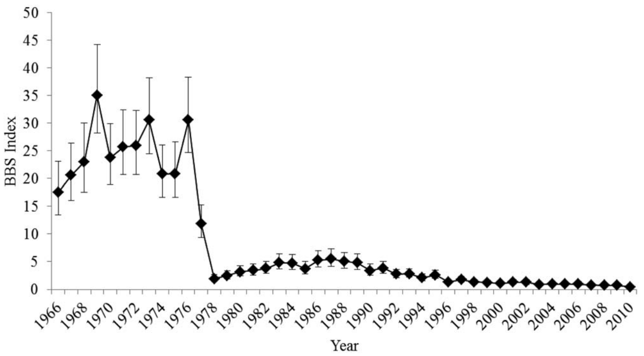

Fig. 1. Population trend of northern bobwhite in Ohio, USA, during 1966–2010 based on the North American Breeding Bird Survey (BBS) Index. The figure includes the BBS Index and 95% confidence interval (Sauer et al. 2014).

The ODNR released F1 bobwhites throughout the state in areas perceived to have suitable habitat and scarce or nonexistent bobwhite populations. F1 bobwhites were released in groups of 20 with a 1 : 1 sex ratio. Releases occurred during late winter or early spring to minimize winter losses while allowing bobwhites time to acclimate to new surroundings before the onset of breeding activity (Urban 1978). Some autumn releases occurred when F1 production exceeded the capacity of holding pens. The ODNR released >65,000 F1 bobwhites in ≥83 Ohio counties throughout 1980–1986. The ODNR utilized the North American Breeding Bird Survey (BBS) and a Rural Mail Carrier (RMC) survey to monitor bobwhite population changes during the F1 program. Gradual increases in the BBS index occurred in the 1980s (Fig. 1) and in 1984 the ODNR reopened quail hunting season in select counties in southwestern Ohio. Yet, the ODNR did not observe anticipated improvements in quail numbers and distribution, which prompted questions about whether F1 bobwhites were contributing to wild recruitment.

In 1984 the ODNR initiated a 2-year study to quantify the contribution of F1 releases to the wild bobwhite population. Henry and Shipley (1989) compared the survival and reproduction of F1 ($n = 100$) and wild translocated ($n = 40$) bobwhite hens fitted with bib-mounted very high frequency transmitters. Within each cohort (F1 and wild) groups of 20 hens were released on 4 study sites over 2 consecutive autumn and spring periods during 1984–1986. Wild hens were released >50 miles (~80 km) from capture locations. Postrelease movement by F1 and wild hens did not differ (0.5 km and 1.6 km, respectively). Apparent survival of F1 hens to 10 weeks postrelease was comparable between autumn and spring release periods (12.8% and 8.5%, respectively). Survival of wild hens was higher following a spring release than an autumn release (36.9% and 17.3%, respectively). Henry and Shipley (1989) suggested this was evidence of a positive survival advantage associated with wild hen maturity. F1 and autumn released wild hens experienced heavy mortality (>50%) during the first week postrelease, whereas spring released wild hens showed only 20% mortality over the same period. Within both cohorts, evidence of nesting was limited to hens released in the spring. Henry and Shipley (1989) found no difference between cohorts in the time between release and the start of incubation (44 days and 47 days for F1 and wild hens, respectively). The timing of nest initiation corresponded with established bobwhite nesting periods in Ohio, irrespective of cohort or release date. Of the F1 hens, a single individual was known to have hatched a clutch, although the hen was predated 1 week after hatch. Of the wild hens, 6 clutches were produced, 2 of which were observed with hens ≥4 weeks posthatch. Henry and Shipley (1989) suggested that multiple factors likely contributed to the poor survival and reproduction of F1 hens, including unfamiliarity with a new environment, inadequate conditioning to native foods and cover, and a lack of predator avoidance behavior. Henry and Shipley (1989) considered F1 hens to be considerably less wary than wild hens for a short time postrelease. F1 hens were often found in open areas outside of protective cover and were frequently approached by observers without fleeing. When flushed, F1 hens flew relatively short distances compared with wild bobwhites and often began vocalizing immediately after landing. These behaviors were not observed in wild bobwhites at any time postrelease and were no longer observed in F1 bobwhite beyond 3 weeks postrelease.

Henry and Shipley (1989) determined late spring translocation of wild adult bobwhite held the greatest potential for successful reestablishment within suitable unoccupied habitat. This release group demonstrated higher survival and productivity than other release groups, and was the principal source of recruitment during the study. Important questions remained, including the number of wild bobwhite necessary to establish a self-sustaining population within suitable unoccupied habitat.

Translocation of Wild-caught Bobwhite

Kansas translocation.—Henry (1993) used stochastic population modeling and survival and reproductive parameters determined by Henry and Shipley (1989) to estimate the minimum number of wild adult bobwhites necessary for successful reestablishment through translocation. Henry (1993) estimated that ≥80 bobwhites (40 M, 40 F) per release site were necessary to yield sufficient brood stock (~45 birds) 12 months postrelease. In 1995 the ODNR initiated a study in which wild-caught bobwhites were to be released in groups of 40, 80, and 120, with 3 replicates of each. The ODNR trapping efforts targeted bobwhite strongholds in southwestern Ohio, yet captured insufficient numbers of wild bobwhites to meet these goals. During 1995, 1996, and 1997, only 52, 34, and 84 bobwhites were caught, respectively. Despite falling well short of project goals, captured quail were released within predetermined sites in Knox and Morrow counties (Fig. 2). Roadside whistle-count data from these sites during 1995–1997 are incomplete, but there was no evidence of successful establishment. No bobwhites were detected via whistle counts on the Morrow County site in 1996, 1 year after release. In addition, ODNR biologists described an "absence of quail" (Traylor 1997) on release sites corresponding to declines documented in the 1996 RMC Survey. These regional population declines were attributed to the "difficult winter of 1995–1996" (Traylor 1997). Given the difficulties of trapping wild birds in Ohio, Traylor (1997) suggested that the ODNR investigate out-of-state sources of wild bobwhite.

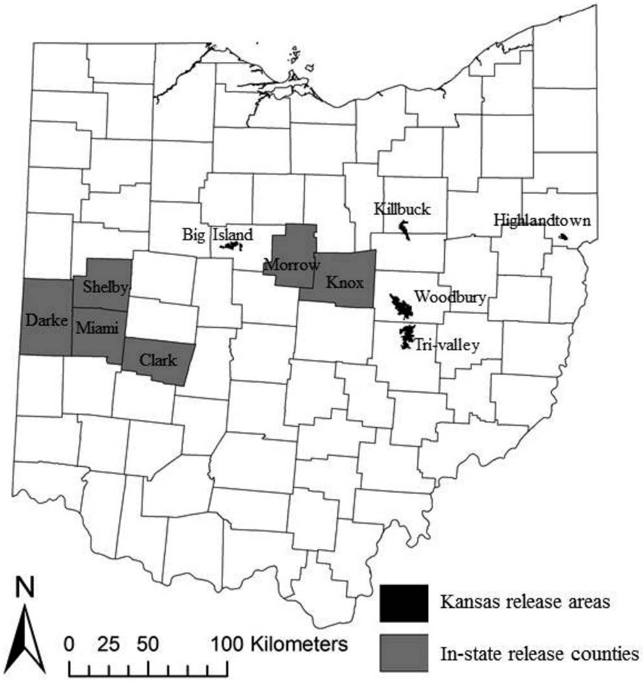

Fig. 2. Release locations for wild-caught northern bobwhite during in-state and out-of-state translocation efforts in Ohio, USA, during 1999–2010.

In 1997, the Kansas Department of Wildlife and Parks (KDWP) agreed to provide the ODNR with wild bobwhite for translocation to large public lands in Ohio. The release locations had no evidence of bobwhite populations and little or no potential for natural colonization. Once established, bobwhites in these areas were intended to serve as source populations for future translocation efforts in Ohio. The first of 2 agreements permitted the ODNR to trap 250 quail annually during 1998–2000. The second agreement permitted the ODNR to trap 250 quail annually during 2005–2008. Although the 250 bobwhites/year would have permitted the ODNR to examine previously established release goals of 40, 80, and 120 birds, the 1995 investigation of stocking rates was apparently abandoned while Henry's (1993) recommendation of ≥80 birds/release was embraced.

Trapping efforts were focused on 2 areas in east-central Kansas. Bobwhites were captured using baited funnel traps and were held in Kansas for up to 4 weeks until a sufficient number (~100) were ready for transport to Ohio via aircraft. During the initial trapping period in 1998, 155 bobwhites were captured and transported to the 19,246-acre (~7,789-ha) Woodbury Wildlife Area

Fig. 3. Whistling male northern bobwhite heard per stop on 5 State Wildlife Areas in Ohio, USA, during the years following release of wild-caught northern bobwhite from Kansas, USA. Surveys were conducted during 1999–2012.

(Woodbury) in Coshocton County for release. During October–November 1999, 180 bobwhites were captured in Kansas and released at the 5,872-acre (2,376-ha) Big Island Wildlife Area (Big Island) in Marion County. During the final trapping period of the first agreement 163 Kansas quail were transported to the 5,671-acre (~2,295-ha) Killbuck Marsh Wildlife Area (Killbuck) in Wayne County (Hull 2001). During late winter 2005, 167 quail were trapped in Kansas and transported to Ohio for release on the 15,181-acre (~6,144-ha) Tri-Valley Wildlife Area (Tri-Valley) in Muskingum County. Bobwhites captured during 2006 were also released on Tri-Valley, while birds captured during 2007 were released on the 2,265-acre (~917-ha) Highlandtown Wildlife Area (Highlandtown) in Columbiana County (Fig. 2). Inclement weather conditions in 2008 were believed to have adversely affected quail populations in Kansas, and the ODNR and KDWP agreed to suspend trapping temporarily. Trapping commenced in 2009 and all birds captured were released at Highlandtown (Stricker 2010).

Spring whistle call-counts and brood surveys were established within release areas to document overwinter survival and estimate productivity. Call-count routes ranged from 10 to 15 stops approximately 0.5 miles (~0.8 km) apart. Routes were initiated on each site following the initial release and were run weekly during the month of June. Observers recorded the number of calling males at each stop for 5 minutes. During August, brood searches were conducted in areas determined to have potential breeding activity based on call-count surveys. Sampling effort and efficiency for the brood survey were not tracked or measured. Brood survey observations were viewed simply as evidence of reproduction with potential for conservative estimates of reproductive success (Hull 2001).

Whistle-count survey results varied somewhat across sites (Fig. 3). In the years following the release at Woodbury, survey results and incidental observations were encouraging. Call-counts recorded 12–25 males during the 4-week survey in 1999 and 24–30 males in 2000. In August 1999, ODNR staff observed approximately 130 individual bobwhites at Woodbury, representing an estimated 10–15 broods produced in the first breeding season postrelease. It was believed brood production was similar on the area in 2000 (Hull 2001). Despite relative stability from 1999 through 2005, whistle counts during 2007–2009 showed marked declines. Roadside surveys within Woodbury detected bobwhite at only 4 of 17 points in 2009 and surveys outside the area found no evidence of quail in the surrounding landscape, although anecdotal sightings of quail off site were reported by wildlife area management staff and local residents.

Whistle count numbers at Big Island were dismal from the onset, though evidence of successful reproduction existed (Hull 2003). Quail numbers apparently remained very low for 4 years postrelease and surveys were discontinued on the area in 2003 (Hull 2005). The ODNR received reports of bobwhite in the vicinity of Big Island in 2006, but believed numbers were insufficient to maintain a viable population (Stricker 2010).

Initial survey results at Killbuck were positive, although detections steadily declined for 5 years postrelease. Surveys did document apparent dispersal from the core release area, which may have contributed to declines. Additionally, inclement winter weather in 2003 was thought to have reduced the population. No bobwhites were detected on surveys at Killbuck during 2006 or 2007, after which surveys were discontinued on the area (Stricker 2007).

The first year (2005) of whistle-count surveys at Tri-Valley produced the highest number of calls per point of any release site. Autumn covey counts detected ≥8 individual coveys (Stricker 2010). Surveys in subsequent years showed considerable declines following years of inclement winter weather. In 2009 the ODNR shifted field-dog-trial activities to Tri-Valley from Killdeer Plains Wildlife Area in Wyandot County. The ODNR had concern field-dog-trial activities might threaten the viability of the nascent bobwhite population on Tri-Valley and made efforts to translocate wild bobwhites from Tri-Valley to Woodbury. Although 5 individual coveys were located on Tri-Valley, only 17 bobwhites were captured before trapping efforts had to be terminated at the start of field trial activities.

Initial whistle-count results at Highlandtown were lower than all sites except Big Island, but counts remained fairly steady for 3 years. Additionally, detections suggested that bobwhites had dispersed throughout the area, including onto surrounding private land. Unfortunately, evidence of bobwhites at Highlandtown disappeared shortly after a severe winter weather event in northeastern Ohio and surveys on this area were discontinued.

In-state translocation.—In 2001, Hull (2001) cautioned that despite positive results in initial years, multiple years of monitoring would be required to determine whether sustained populations had been established through translocation. Yet, the ODNR initiated an in-state translocation effort in 2002 based largely on the perceived success at Woodbury (Hull 2003). The objective of this effort was to trap wild bobwhite in the core of the Ohio range and release them to nearby counties, which supported wild quail as recently as the

Table 1. Mean number of whistling northern bobwhite males heard per stop at release sites in years following initial release of wild-caught northern bobwhite from southern Ohio, USA, 2002–2012. '—' indicates route was not run.

Release site	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
SHEL1	0.70	1.30	2.41	3.26	2.25	0.86	2.17	2.73	1.80	0.00	0.00
DARK1		0.33	0.63	0.40	1.27	0.70	0.78	0.56	0.27	—	0.02
MIAM1			0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SHEL2				0.42	0.25	0.14	0.12	0.06	0.03	—	0.00
CLAR1					0.70	0.48	0.11	0.04	0.07	0.00	0.00
CLAR2						0.30	0.04	0.07	0.00	0.00	0.00
DARK2							1.00	0.13	0.00	—	0.00
SHEL3									0.00	0.00	0.00
MIAM2										0.00	0.03

early 1990s but no longer had evidence of bobwhite populations.

The ODNR captured bobwhites on public and private property in southwestern Ohio during winter using baited funnel traps. All bobwhites captured were kept at a holding facility at Spring Valley Wildlife Area in Greene County until an adequate number of birds were obtained for release (90–125). Bobwhites were released at a new release site each year. Supplemental feed was provided at the release site to keep the bobwhites localized for several days postrelease. Trapping occurred in Brown, Butler, Highland, and Preble counties and releases occurred on 8 sites determined to have suitable habitat in Clark, Darke, Miami, and Shelby counties. Suitable habitat was defined as 50% grassland and 10–20% brushland at the township scale (Frevert 2007). Within the selected townships, release sites were chosen by ODNR staff based on the quality and quantity of contiguous bobwhite habitat available, as well as the presence of linking corridors (i.e., riverine watersheds). Release sites were located on private property and were >3.7 miles (~6.0 km) apart (D. Malas, personal communication) All release sites were within counties closed to bobwhite hunting. During 2002–2011, 795 total bobwhites were relocated to 8 release sites.

The ODNR monitored in-state translocation release sites using midsummer call-count surveys and late-summer brood surveys similar to those used on Kansas translocation sites (Hull 2003). Several broods were detected by ODNR staff and private landowners 1 year postrelease in Shelby County, but it is unclear whether brood surveys were continued after 2002. The results of whistle count surveys in these areas were mixed and show very few bobwhite detections 5 years postrelease in most release sites. Only sites "Shelby Co. 1" and "Darke Co. 1" had strong evidence of population persistence beyond 5 years. In 2011, no bobwhites were detected during any surveys, though 3 routes were not run (Table 1). During 2012, 2 whistling bobwhites were detected on all routes combined and whistle counts were discontinued shortly thereafter.

DISCUSSION

In the late 1970s, the ODNR conceded that artificial propagation and translocation could be justified where wild stock was severely depleted by temporary causative factors (e.g., weather) leaving suitable bobwhite habitat unoccupied with little potential for natural recolonization (ODNR 1984). The ODNR cited ≥2 studies that showed abnormally low population levels caused by irregular occurrences could be improved through the release of hatchery stock (Brill 1941, Duck and Fletcher 1944). The ODNR deemed the release of commercial hatchery stock inappropriate because the circumstances and conditions under which birds are bred and reared likely eliminated many of the physical and behavioral qualities necessary for survival in the wild. The ODNR believed the introduction of hatchery stock could seriously damage the existing gene pool given the extremely low number of remnant wild birds in the state (Urban 1978). The ODNR considered translocation of wild-caught bobwhite preferable, but this method was not feasible given the quantity of bobwhites needed far exceeded the number that could be caught. Wild translocation at a statewide scale was thought to be an economic and logistic impracticality for the agency (Henry and Shipley 1989). Captive propagation of wild-caught bobwhites and the subsequent release of F1 progeny were feasible solutions to these issues (Urban 1978). F1 bobwhites were produced in relatively large quantities, and met the established release goal of 10,000 birds released/year statewide. Additionally, F1 bobwhites maintained near-wild genetic expression. In theory, F1 bobwhites possessed the most innately determined behavioral attributes achievable in a captive-reared bobwhite (Henry and Shipley 1989).

Backs (1982) found that F1 bobwhites survived for a significantly longer period than did commercial hatchery stock following spring or autumn release into suitable unoccupied habitat, but questions remained about the survival and reproduction of F1 bobwhites relative to translocated wild bobwhites. Henry and Shipley (1989) concluded that F1 bobwhite propagation with regard to genetic wild programming coupled with minimized human contact in rearing was not an effective population restoration strategy. The contribution of innately determined behavioral attributes to overall survival and reproduction in the wild is important, but attributes derived from extrinsic factors are likely to play a large role in determining survival and reproductive potential of released bobwhite (Roseberry et al. 1987, Henry and Shipley 1989). Henry and Shipley (1989) noted that the potential impact of enhanced prerelease conditioning procedures on F1 survival was unknown and merited further investigation.

F1 bobwhites reared and released in Ohio during 1980–1985 likely survived and reproduced at very low levels in many areas of the state. Henry (1993) speculated that failure to reestablish bobwhite populations was the result of an insufficient density of bobwhite in release areas to increase natality to the point of population growth and expansion. He questioned whether 20-bird releases were adequate in light of known rates of loss (e.g., mortality, dispersal). In 1993, Henry completed a thorough literature review on bobwhite translocation and consulted with biologists involved with translocation efforts within multiple states. Across the species' range, methods varied and opinions differed about the value of bobwhite translocation.

The ODNR's efforts throughout the past several decades show no evidence that translocated populations persist. It is probable Ohio's various bobwhite translocation efforts during 1978–2012 produced small isolated populations that were extremely vulnerable to stochastic extinction in the years immediately following initial release. Throughout this period numerous observations suggested that inclement winter weather was detrimental to nascent populations. Even within areas perceived to contain large amounts of suitable habitat, the impact of stochastic events may have been exacerbated by the isolation of the populations. The ODNR has achieved success in reintroduction of other species (e.g., wild turkey [*Meleagris gallopavo*]), but has no evidence that propagation and translocation efforts in recent decades had any measurable effect on statewide bobwhite abundance or distribution. Recent population indices reflect continued declines and range contraction, even within population strongholds in southwestern Ohio.

Translocation of wild-caught bobwhite appears to offer the greatest potential for successful population establishment through artificial means. It is yet unclear whether Henry's (1993) recommendation of 80 bobwhites is sufficient and bears continued investigation where feasible. It may be necessary to consider repeated releases on the same site in consecutive years to bolster newly established populations, increase density, and increase natality to the point of population growth. Dispersal from newly released populations was noted on several sites either through formal surveys or anecdotally. Dispersal from established bobwhite populations has been studied in the past, but it is unclear the degree to which dispersal was included in Henry's (1993) efforts to model quail population viability and stocking rates. We suspect that such movement of individuals away from novel, isolated populations should not be dismissed without consideration of the implications for population establishment and viability, especially where dispersal into hostile landscapes is likely.

MANAGEMENT IMPLICATIONS

Some tentative conclusions that can be drawn from Ohio's efforts to propagate and translocate wild bobwhites include 1) translocation of wild-caught bobwhites likely offers the greatest potential for successful population establishment in areas devoid of bobwhite; 2) along with high mortality and reduced reproductive rates, emigration may be a factor contributing to failure of translocated bobwhite populations isolated from existing populations; 3) population monitoring should occur in and around release sites for a minimum of 7–10 years and wildlife managers should remain circumspect in their assessment of success; 4) minimum stocking rates and annual stocking supplements need continued consideration.

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THE EFFECT OF AGE-AT-RELEASE ON SURVIVAL OF ADOPTIVE PARENT-REARED BOBWHITE CHICKS

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ABSTRACT

Translocation of wild northern bobwhites (*Colinus virginianus*) to restore local populations is a viable conservation tool under some scenarios; however, the supply of wild bobwhites is limited. Bobwhites can be artificially propagated, as an alternative to translocation, using methods that mimic natural brood-rearing. The parent-rearing adoptive process (PRAP) uses wild-strain bobwhite adults to brood and foster newly hatched wild-strain chicks in outdoor aviaries that emulate a natural environment. Adoptive parent-reared bobwhites have higher survival rates than artificially-reared bobwhites but only a single age-of-release (i.e., 6-weeks) has been tested. We tested the effect of age-at-release (3, 6, and 9-weeks) on adoptive parent-reared chicks released on the same date in Hanna Hammock of Tall Timbers Research Station. All chicks were marked with patagial wing tags and a subset of the group received radio transmitters. The 3-week-olds ($n = 25$) received suture-style transmitters and 6-week-olds ($n = 30$) and 9-week-olds ($n = 30$) received necklace-style transmitters. Our adoptive parent-reared chicks had low survival rates over 3 months post-release, the 9-week age group had the highest overall survival rates which could portend that increased physiological development may aid in increasing the survivability of adoptive parent-reared bobwhites. The low survival rates across all 3 age classes calls into question the efficacy of the PRAP as a bobwhite restoration method. Our results do suggest that additional modifications to release age ($>$ 9-weeks) should be explored along with further modifications to the PRAP. Additional modifications include incorporating predator avoidance training, altering release dates, and changing nutritional regimes. These results should caution the bobwhite community to remain suspect when deriving conclusions about the PRAP until all process modifications have been fully evaluated by scientific research.

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Key words: artificial propagation, age effects, chicks, *Colinus virginianus*, northern bobwhite, parent-reared, Red Hills, reintroduction, restoration, Tall Timbers Research Station

Northern bobwhite (*Colinus virginianus;* hereafter bobwhites) populations have been in continual decline at a rate of 4.2% per year during 1966-2015 (Sauer et al. 2015). The primary reason for the decline in bobwhite populations has been broad-scale habitat loss, habitat degradation through advancements in agriculture technology as well as afforestation and lack of prescribed fire (Brennan 1991). In response, habitat restoration (Palmer et al. 2012) and restocking efforts have been undertaken in many parts of the bobwhite range (Buechner 1950, Perez et al. 2002, Jones 2004, Cass 2008, Terhune et al. 2010). In spite of these efforts, landscape level change has reduced the quality and quantity of habitat for bobwhites, which has resulted in localized and even regional extirpations (Guthery 1999, Veech 2006). The anthropogenic influence on the landscape has heightened habitat fragmentation, habitat isolation and decreased landscape permeability, thus reducing colonization and recolonization rates (Bowling et al. 2014). These factors underscore the need for understanding how reintroduction techniques can aid bobwhite restoration and to identify limitations as a means to recover populations.

A variety of bobwhite reintroduction methods have been employed to establish, reestablish or augment bobwhite populations across their range, including both captive-reared (e.g., pen-reared and Surrogator® systems) and wild translocation programs. The value of releasing pen-reared birds to supplement hunting stock is commonly acceptable but this technique is not an effective population restoration tool (Buechner 1950, Devos and Mueller 1989). Numerous studies have documented low survival rates of pen-raised bobwhites (Baumgartner 1944, Roseberry et al. 1987, DeVos and Speake 1995, Oakley et al. 2000, Hutchins and Hernández 2003) and

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their potential adverse effects on survival rates of wild bobwhites by predators attracted to release areas is further cause for concern (DeVos and Speake 1995). Similarly, birds reared in Surrogators had low overall survival rates (0.35) over 8-weeks after release (Thacker et al. 2016). The limited proportional return (0.005; 19 marked harvest returns from 3859 marked total releases) of Surrogator birds to hunter bags over a 5-year study conducted in Alabama, Georgia, and Kentucky not only diminishes the possibility of the Surrogator as a viable option for population recovery but also calls into question its use for stock supplementation for hunting purposes (Thackston et al. 2002).

Translocation of wild bobwhites after habitat restoration has been successfully used to recover and augment existing wild populations (Terhune et al. 2006a, 2010). Terhune et al. (2006b) found that resident and translocated bobwhites had similar survival rates, reproductive effort, and daily nest survival rates. Translocated and resident bobwhites also had similar home range sizes and mean daily movement distances (Terhune et al. 2006b, 2010). These results indicate that translocation of wild bobwhites can be a reliable method to restore bobwhite populations. However, source populations of wild bobwhites are limited (Martin et al. 2017) and the financial constraints of wild bird translocations is high (Sisson et al. 2017). Therefore, the efficacy of translocation for broad-scale population recovery is limited.

Recognizing the limitations of translocation and the need for population recovery through restocking, the Game Bird Program at Tall Timbers Research Station and Land Conservancy began investigation of a technique to foster wild-strain birds with learned cues from adoptive parents. Stoddard (1931) was one of the first to experiment with this type of artificial propagation of bobwhites in the mid-to-late 1920s. He used bantam chickens (*Gallus gallus*) as brooders, male bobwhites as foster parents, and released the birds to the wild – he called this process the adoption system of rearing. Similarly, Tall Timbers' method used F1 birds (or first generation removed from true wild stock) as foster parents coupled with hen vocalizations before and after hatching to increase adoption rates. Adult birds were removed after 5–7 weeks and chicks were wing-tagged and released on sites with high quality habitat during July-October depending on latitude and coinciding with natural peak hatching in the wild. Initial investigation of the success of this technique was has shown promise (Palmer et al. 2012). Survival to the following spring for bobwhite chicks reared using the PRAP (parent-reared adoptive process) ranged from 0.035–0.111 in 2005, and 0.128–0.262 in 2006 for July, August, and September releases in each respective year (Cass 2008). However, mixed results have been observed with replication of the PRAP (Palmer et al. 2012, Macaluso et al. 2017, D.C. Sisson, personal communication). Current research has shown some improvement in survival rates over traditional pen raised, artificially brooded bobwhites thus warranting further research into the PRAP.

We tested the effect of age-at-release on post-release survival of adoptive parent-reared bobwhite chicks. We hypothesized that modification of age-at-release will have an effect on the survival of adoptive parent-reared chicks. We predicted that survival rates would decrease with age if human habituation is the strongest effect. Conversely, we predicted survival rates would increase with age if physiological development is the strongest effect. Adoption rates may vary by chick age at release into the wild and differences in physiological development (increased wing and leg development) among ages (i.e., cognitive ability) may impact survival. We predicted that 3-week-old adoptive parent-reared chicks would have higher survival rates due to adoption by wild adults (Faircloth et al. 2005). Our intent for this research was to modify the parent-rearing system to achieve higher survival rates and productivity resulting in a more robust population recovery tool.

STUDY AREA

We released adoptive parent-reared chicks in the Hanna Hammock section of Tall Timbers Research Station located in the Red Hills Region approximately 33.5 km north of Tallahassee, Florida. Aviaries were located in Hanna Hammock and the Tower Course tract of Tall Timbers Research Station. The habitat in Hanna Hammock is similar to the rest of the Tall Timbers property, primarily comprised of old-field upland pine with a mix of shortleaf (*Pinus echinata*), loblolly (*Pinus taeda*), and longleaf (*Pinus palustris*) and an understory consisting of sweetgum (*Liquidambar styraciflua*), American beautyberry (*Callicarpa americana*), and a variety of grasses and forbs including little bluestem (*Schizachyrium scoparium*) and common ragweed (*Ambrosia artemisiifolia*). The property is intensively managed for bobwhites which includes prescribed fire, timber harvesting, herbicide application, supplemental feeding, and seasonal predator control. The upland pine section of Hanna Hammock is approximately 94 hectares and is bounded on its east and west sides by hardwood drains leading down to Lake Iamonia. Hanna Hammock is the western-most section of Tall Timbers that is intensively managed for bobwhites. Hanna Hammock is separated from the main portion Tall Timbers by a large hardwood drain. Tall Timbers Research Station currently practices "strict wild bird management" which prohibits the release of artificially-reared bobwhites anywhere on the main portion of the property. However, the Hanna Hammock tract of Tall Timbers has had releases of artificially reared bobwhites in the past in an attempt to augment the current population.

METHODS

Aviaries

Aviaries (Tower Course and Hanna Hammock) were constructed away from high traffic areas to minimize any human habituation and tampering with birds throughout the rearing process. Both sets of aviaries used wood framing for pen construction and walls were enclosed with poultry netting. Aviaries were also fortified to prevent intrusion of snakes by burying wood framing below ground level. Both aviaries contained natural vegetation (*Callicapra americana* and *Rubus* spp.) to imitate natural brood-rearing habitat. The Tower Course aviaries followed the design used by Stoddard (1931). This design used trapezoidal-shaped pens with brooding houses located on the narrower section to facilitate capture and removal. The aviaries were covered with netting and about half of each pen was covered with vinyl roofing to prevent mortality associated with severe rain events. The Hanna Hammock aviaries were rectangular in shape with brooding/feeding houses located at the front of each aviary. Aviary walls were covered with shade cloth to limit visibility in hopes of minimizing human habituation during the rearing process. Aviary rooftops were also constructed using netting and shade cloth to minimize sunlight, decrease visibility, and reduce rainfall impact.

Rearing Process

Quail Call Farms (Beachton, GA) provided all eggs used in our study. We used F1 eggs indicating that the parents of each egg are only one generation removed from wild bobwhites. Eggs from wild bobwhites were collected from partially depredated and abandoned nests at Tall Timbers Research Station and other associated properties. These eggs are hatched in captivity to produce breeders so that wild genetics can be maintained in release groups. Eggs were collected daily (as they were laid) at Quail Call Farms from each laying hen in a captive wild-strain breeding stock. Incubation periods were initiated on select dates (9-Week Age Class: 04 June 2015, 6-Week Age Class: 25 June 2015, 3-Week Age Class: 16 July 2015) to ensure that all chicks were the proper age on the day of release (06 Aug 2015). We placed all eggs from each age class in a Model 1500 Series incubator (G. Q. F. Manufacturing Company, Savannah, GA). We relocated eggs to another incubator (G. Q. F Manufacturing Company, Savannah, GA) the day before hatch (Day 22). We also placed the next batch of eggs in the original incubator at this time to maintain a consistent number of chicks. We periodically examined eggs to identify any eggs exhibiting signs of failure (no yellow glow when candled) throughout the incubation process and discarded eggs that did not emit a yellow hue upon examination.

Quail Call Farms (Beachton, GA) provided the adult brooding stock (40–45 captive-reared adults) for each adoption period. We systematically alternated male and female adults during the adoption period to eliminate any bias by only choosing one sex as brooding stock. We placed each brooding adult into the brood boxes prior to the addition of newly hatched chicks. We prepared brooding boxes by placing cedar shavings on the floor of each box prior to each adoption and cleaned all boxes after the adoption period. We selected chicks for adoption by assessing their post-hatch condition (when feathers had begun to dry) and placed approximately 18 chicks with each brooding adult. Chicks and adults were given approximately 10 min to bond before behavioral observations began. We conducted behavioral observations to determine if broods were accepted or rejected by the adult. Adults that exhibited aggressive behavior (pecking, etc.) were immediately removed and placed in a discard box. Adults that approached chicks but did not readily brood chicks were given more time (up to 10 min) to adopt. We attempted to facilitate the adoption process by moving chicks closer to the foster parent if chicks were not being brooded immediately. If the adult did not adopt following manipulation, we then removed the individual and placed another adult with chicks and repeated the process described above. We allowed an additional 5 min of bonding time if adoption occurred immediately, then transferred the brood to a transport box for placement in aviaries. This process continued until all chicks were prepared for release into aviaries.

Aviaries were examined for damages prior to full release. Any aviaries needing repair were fixed prior to release to prevent any chances of escape or mixing of chicks between pens. We prepared brooding houses for the holding period (1–5 days pre-full release) by lining brood house floors with cedar shavings and setting disposable trays filled with gamebird feed (Purina Mills, Gray Summit, MO) and a waterer. We secured brood houses by fastening a wooden door onto house entrances with wood screws until chicks were ready for full-release. We closely monitored weather forecasts until optimal release conditions were predicted (24–48 hours of no rain) after which all chicks were released into aviaries for rearing. Two F1 adults and their respective broods were assigned to each aviary pen (multiple pens per aviary) throughout the rearing period for all age classes. Age groups were unevenly distributed among aviaries. The 9-week group was split between the Hanna Hammock and Tower Course aviaries (Hanna, $n = 26$ & Tower, $n = 4$), and the 6-week group ($n = 24$) were all raised in the Tower course aviary. The 3-week group ($n = 25$) were all raised in the Hanna Hammock aviaries. Age groups did not comingle, and were only reared with adoptive adults and brood mates designated at the beginning of the adoptive process.

We fed chicks and F1 adults a game bird starter feed (Purina Mills, Gray Summit, MO), approximately 28% protein, throughout the rearing process. We scattered proso millet (*Panicum miliaceum*) after 1 week in each aviary (approximately three handfuls per pen each visit) and at 3-weeks of age milo (*Sorgum bicolor*) was scattered with millet at the same rate. Rodents were controlled using Sherman traps (H. B. Sherman Traps, Tallahassee, FL) as needed when holes under brooding houses and aviaries were observed. Red-imported fire ant (*Solenopsis invicta*) mounds were treated them with Amdro, 0.73% hydramethylnon, (AMBRANDS, Atlanta, GA). All care, rearing, and housing of adoptive parent-reared chicks were in compliance with Tall Timbers Institutional Animal Care and Use Committee (GD - 2001-15).

Release

We organized release groups into 4 single-age aggregations (3-, 6-, and 9-weeks) and 4 mixed-age groups of 15 (5 per age class in each group) prior to release. These aggregations were released at 16 sites across Hanna Hammock. We used ArcGIS (ESRI, Redlands, California, USA) to place a 200 × 200 m grid over the entire study area, and then generated two random points per grid block using the "Create Random Points" tool in ArcGIS. Two-hundred meter grids were used to ensure release sites. Random points were generated with a 40-m buffer using the "Buffer" tool in ArcGIS to allow for the selection of optimal release sites. Random points were visited by researchers to determine optimal release sites and one random grid block was chosen. The 40-m buffer allowed researchers to select release sites that avoided undesirable landscape features such as roads, hardwood drains, plowed fields, or any other open areas that lacked vegetative cover for concealment. Optimal sites were determined by presence of nearby escape cover (woody vegetation), proximity to feed line, and proximity to hardwood drain. A random number generator was used to assign chick groups to release sites.

Brooding adults were separated from chicks before data collection and attaching transmitters or wing tags. We weighed all adoptive parent-reared chicks prior to release. We attached patagial wing tags to all adoptive parent-reared chicks on the day of release (6 Aug 2015). We used wing banding pliers to affix tags to the right wing of all chicks. Each patagial wing tag contained a unique ID for each chick that included year, band series number, and ID number for each respective chick. We fitted necklace-style radio collars (3.5 g American Wildlife Enterprises, Monticello, FL) to 6 ($n = 24$) and 9-week-old ($n = 30$) adoptive parent-reared chicks, and we sutured transmitters (0.7 g American Wildlife Enterprises, Monticello, FL) onto the interscapular region of 3-week-old chicks ($n = 25$) due to their smaller size (Terhune et al., unpublished data). All transmitters were attached on the day of release. All release groups were liberated using a 'soft release' technique. We placed chicks in fruit crates, scattered grain (millet and milo) around release areas, and removed one end of the fruit crate after it was placed in cover so chicks could slowly leave the crate and assimilate to the area.

Telemetry

We located radio-marked chicks every day for the first 28 days after release, and 3 days per week thereafter. We used hand-held 3-element Yagi antennas and ATS Telemetry Receivers (ATS, Isanti, MN, USA) to locate birds over the duration of the study. We recovered radio collars immediately to determine the cause of mortality when transmitters emitted mortality signals. Mortality causes were determined by analyzing evidence (plucked feathers, chewed transmitter, etc.) discovered at kill site, and assigning appropriate fates (mammal, avian, etc.) (Dumke and Pils 1973).

Survival Estimation and Data Collection

Survival estimates for our study period were estimated during 6 August 2015 to 11 November 2015 (97 days) to determine how many individuals survived to fall. Birds that left the release area or were lost due to transmitter failure were right-censored from the study sample. We used the known fates model in Program MARK (White and Burnham 1999) to analyze survival data. We used the logit-link function to restrict survival probabilities between 0 and 1 (Paasivaara and Pöysä 2007). We used *a priori* hypotheses to develop 9 candidate models proposed to explain the variation in survival rates of parent-reared bobwhites (Burnham and Anderson 1998, Johnson and Omland 2004). We tested effect of age on survival rates of parent-reared bobwhites. We also included variables that potentially affected survival rates including aviary, release group, linear time, and quadratic time. Age was separated into three dummy variables (Age3, Age6, and Age9) where each bird was coded a 1 in its respective age group and a 0 if not. Aviary was modeled as a dummy variable where birds were coded a 1 if they were reared in the Hanna Hammock aviaries and a 0 if not. Group Type (single or mixed age) was included as a covariate to determine the effect of group type on survival rates. Birds were coded a 1 if they were released in a mixed-age group and a 0 if they were released in a single age group. We included time variables (linear and quadratic) to examine if there was time variation in survival rates throughout the study period. The best approximating models were chosen using Akaike's Information Criterion (AICc) and we considered the model with the lowest AICc value to be the best approximating model (Burnham and Anderson 1998). The selection of best approximating models was based on ΔAICc values calculated in program MARK as the differences in current AICc value and the minimum AICc value. Relative plausibility of each model was assessed using Akaike weights, w_i (Burnham and Anderson 1998, Anderson et al. 2000), where the best models had the highest Akaike weights. We used model averaging across our entire candidate model set to derive daily survival rates (DSR) for each age class (Akaike 1974, 1978; Burnham and Anderson 1998). We also reported beta estimates, their standard errors, and 95% confidence intervals to allow for stronger inference and comparison among covariates. Probabilities for surviving the study period were calculated in MARK (White and Burnham 1999) and included in the derived estimates from our top candidate models. Cause-specific mortality percentages were calculated by dividing the total number of mortalities by each type by the total number of mortalities for each age class.

RESULTS

Mortality rates were highest during the first three weeks post-release with 70 observed mortalities over this period. Only two 6-week and 12 9-week-old adoptive parent-reared bobwhites remained on the study area after the first 3 weeks. The majority of 6-week-old mortalities

Table 1. Akaike's Information Criterion rankings for models approximating the daily survival rates of adoptive parent-reared bobwhite chicks released in the Hanna Hammock section of Tall Timbers Research Station, Tallahassee, FL, USA, 2015.

k	Model	AICc	ΔAICc	wi	Model Likelihood	Deviance
5	Age+LinTime+QuadTime	493.6752	0	0.33195	1	483.6143
4	Age+LinTime	495.036	1.3608	0.1681	0.5064	486.9954
6	Age+Group+LinTime+QuadTime	495.496	1.8208	0.13356	0.4024	483.4106
6	Age+Aviary+LinTime+QuadTime	495.6203	1.9451	0.12552	0.3781	483.535
5	Age+Group+LinTime	496.7247	3.0495	0.07226	0.2177	486.6638
5	Age+Aviary+LinTime	496.7884	3.1132	0.06999	0.2108	486.7275
3	Age	497.2477	3.5725	0.05563	0.1676	491.2234
4	Age+Group	499.0965	5.4213	0.02207	0.0665	491.0559
4	Age+Aviary	499.208	5.5328	0.02088	0.0629	491.1675
1	Null	513.1082	19.433	0.00002	0.0001	511.1041
2	Aviary	514.034	20.3588	0.00001	0	510.0219
2	Group	514.6537	20.9785	0.00001	0	510.6416

occurred within 6 weeks of release and all but 4 birds survived for more than 2 weeks after the release date. Compared to 3-week-olds (0.68) and 6-week-olds (0.67), the 9-week-old group had much lower mortality rates (0.2) in the first 7 days following release.

Our most parsimonious model included the effects of age, linear time, and quadratic time. Three of our 4 top candidate models included all three of these variables along with aviary and group effects and our second competing model only contained the effect of age and linear time (Table 1). Based on model weights, our top model approximated survival estimates were nearly 2 times better than our second candidate model [Age + LinTime] (0.332/0.168), 2.5 times better than our third competing model [Age + Group Type + LinTime + QuadTime] (0.332/0.134), and 2.6 times better than our fourth competing model [Age + Aviary + LinTime + QuadTime] (0.332/0.126) (Table 1). The sum of the Akaike weights of models containing the effect of Age, Linear Time, and Quadratic Time totaled 0.75 (Table 1), indicating these three variables were important factors in our data set. Model-averaged Beta coefficients indicate that age had an effect on DSR of adoptive parent-reared chicks, along with linear time. The 95% confidence intervals of the remaining beta coefficients (quadratic time, aviary, and group) overlapped zero indicating their effects were uninformative (Table 2).

Table 2. Beta coefficient estimates for all included covariates from our model-averaged set approximating daily survival rates of adoptive parent-reared bobwhite chicks released in the Hanna Hammock section of Tall Timbers Research Station, Tallahassee, FL, USA, 2015.

Parameter	β	SE	95% LCI	95% UCI
Age9	3.71	0.50	2.72	4.70
Age3	-1.76	0.41	-2.57	-0.95
Age6	-1.14	0.43	-1.99	-0.30
LinTime	-0.05	0.03	-0.10	-0.01
QuadTime	0.00	0.00	-0.00	0.00
Aviary	-0.22	0.64	-1.47	1.03
Group	-0.13	0.26	-0.64	0.38

Our model averaged results for daily survival rates (hereafter DSR) for each age class indicated low survival rates for our 3-week age group (DSR = 0.827, SE = 0.422, 95% CI: 0.113–0.994; Fig. 1) and 6-week age group (DSR = 0.898, SE = 0.458, 95% CI: 0.186–0.997; Fig. 1). Our 9-week group experienced higher DSRs over the course of the study (DSR = 0.965, SE = 0.492, 95% CI: 0.625–0.998; Fig. 1). The probabilities for surviving study period (14 weeks) were marginally above zero for all age classes (3-week: 0.578E-13, 6-week: 0.137E-06, 9-week: 0.005).

Avian (*n* = 8, 32%) and mammalian (*n* = 7, 28%) predators contributed almost evenly to sources of mortality for 3 week-old chicks. Other mortalities were classified as unknown due to lack of evidence at kill site (*n* = 8, 32%) and snake depredations (*n* = 1, 4%). One 3-week-old was censored due to unknown fate or possible collar loss. Mammals were the leading cause of mortality among the 6-week age group (*n* = 11, 46%). Other causes of mortality for the 6-week age group include avian (*n* =

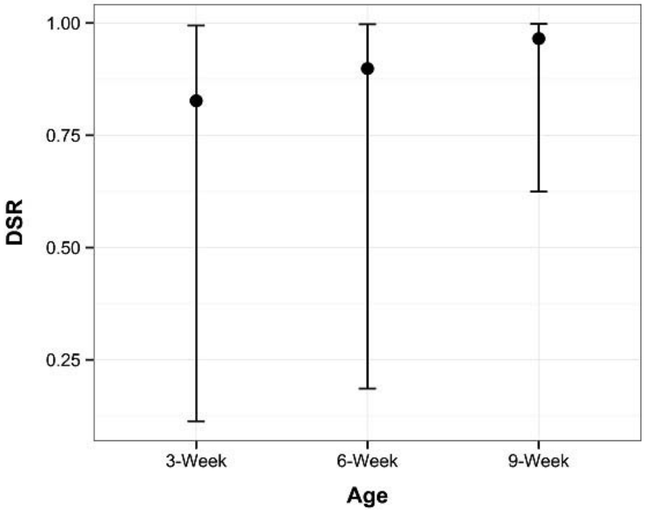

Fig. 1. Model-averaged daily survival estimates (DSR) (error bars represent 95% confidence intervals) for 3-, 6-, and 9-week old adoptive parent-reared bobwhite chicks released in Hanna Hammock, Tall Timbers Research Station, 6 Aug 2015 to 11 Nov 2015.

8, 33%), snake ($n = 1$, 4%), transmitter-related ($n = 1$, 4%), and unknown due to lack of evidence ($n = 3$, 13%). The mortality causes for 9-week age group were mammalian ($n = 15$, 50%), avian ($n = 9$, 30%) and unknown due to lack of evidence ($n = 3$, 10%). The fates of 3 9-week-olds were unknown and were censored from the sample.

DISCUSSION

Our results indicate that a high level of mortality should be expected for adoptive parent-reared bobwhites, especially during the first few weeks post-release. The higher survival rates observed in our oldest age class indicate that age has some effect on survival rates of adoptive parent-reared bobwhites after release. This could indicate that increased physiological development prior to release confers survival advantages. The extremely low survival rates of 9-week old PRAP chicks does not portend success of this method as a population restoration technique.

The low overall survival rates for our chicks was consistent with other studies examining survival rates of captive-reared bobwhites (Baumgartner 1944, DeVos and Speake 1995, Oakley et al. 2000, Hutchins and Hernández 2003). Survival rates for our 6- and 9-week old age classes was lower (all studies) than reported by Palmer et al. (2012). A study of PRAP bobwhites (5–8 weeks in age) near our study area found over-winter survival was 0.14 (0.08–0.44 95% CI) and 0.3 (0.19–0.41 95% CI) in 2005 and 2006 (Cass 2008). Additionally, survival of adoptive parent-reared chicks to spring varied from 0.03-0.11 and 0.12–0.26 in 2005 and 2006 (Cass 2008). Breeding season survival of PRAP bobwhites in South Carolina was 0.27 (0.15–0.39 95% CI) (Palmer et al. 2012). Survival to the next breeding season and producing viable offspring is the ultimate metric by which the success of PRAP should be judged in the short-term. Released individuals surviving to and through breeding seasons can reproduce successfully and contribute to population growth. Palmer et al. (2012) found that parent reared bobwhites were able to produce 0.29 and 0.33 nests per hen in 2006 and 2007 on their Georgia site and 0.64 nests per hen on their South Carolina study site. Parent-rearing has also been tested in red-legged partridges (*Alectoris rufa*). The average survival periods for adoptive parent-reared red-legged partridges did not significantly differ from wild partridges (107.8 ± 20.9 days vs. 160 ± 19.4 days) (Pérez et al. 2015). Natural rearing, a rearing method that allows captive birds to freely choose mates, nest, and brood in a large aviary amongst other captive pairs, also improved re-sighting rates (Natural = 0.23 vs. Artificial = 0.00) of red-legged partridges when compared to artificially reared (incubator hatched and artificially heated) partridges over a 6-month period (Santilli et al. 2012). As such, factors other than age-at-release such as weather (heat, abundant rainfall, etc.) and predator dynamics may better elucidate the success of the parent-rearing adoptive system.

A possible reason for the high mortality rates experienced in our study is the lack of proper anti-predator behaviors imprinted on chicks during the rearing process (Beani and Dessi-Fulgheri 1998). Chicks were reared in pens with all precautions taken to eliminate any opportunity for chicks to encounter predators while being brooded. High mortality rates among released adoptive parent-reared bobwhites may indicate limitations of the rearing system to provide proper cognitive abilities and encourage physiological development among adoptive parent-reared chicks (Pérez et al. 2015). Other studies have documented behavioral differences and predator vigilance of captive-reared and wild bobwhites (Jung and Hayslette 2016). There were significant differences in mean flight speeds of released wild and captive-reared bobwhites in south Texas (Perez et al. 2002) offering some evidence that differences in physiological development may impact survival rates. Reactions to predator stimuli differed among captive-reared and wild bobwhites in a study conducted in north Texas (Newman 2015). Captive-reared bobwhite tended to flush when exposed to terrestrial and raptorial threats during attack simulations, while wild bobwhite tended to freeze or run, suggesting that these behaviors are absent in captive-reared bobwhites (Newman 2015). The tendency for captive-reared bobwhites to immediately flush in reaction to predator stimuli reveals the location of a bird to a predator (potentially easing subsequent predation attempts), which may explain the low survival rates of captive-reared bobwhites after release (Newman 2015). Differences in threat responses have also been observed in other galliformes. Flush distances in response to an approaching human and trained dog were greater for wild greater prairie-chickens (*Tympanuchus cupido*) than pen-reared Attwaters's prairie chickens (*T. cupido attwateri*) (Hess et al. 2005). The lack of these behaviors suggest that artificial rearing systems may cause an ethological and physiological deficit for game birds raised in captivity (Pérez et al. 2015). Maximizing survival of released individuals will ultimately increase breeding opportunities in the future and assist in establishing populations more effectively (Hardman and Moro 2006). The extremely high mortality rates experienced by chicks in our study limits the efficacy of the PRAP technique to establish viable bobwhite populations.

Future studies of adoptive parent-reared systems should include testing earlier release dates (prior to August) and behavioral conditioning. Anti-predator conditioning may trigger anti-predator/predator evasion responses deficient in adoptive parent-reared chicks. Anti-predator training worked with houbara bustards (*Chlamydotis undulata*) when reared birds were exposed to a live red fox (*Vulpes vulpes*) prior to release indicating that the development of anti-predator behavior may increase post-release survival (van Heezik et al. 1999). We expected habituation through extended periods in aviaries, but 9-week old chicks had higher survival rates potentially warranting the evaluation of releasing of older birds. Planting artificially hatched chicks with surrogate parents has been successfully tested with sage grouse (*Centrocercus urophasianus*), with adoption rates of

0.887 over three breeding seasons (Thompson et al. 2015). High rates of brood amalgamation and adoptions among bobwhites has been documented in the past and may allow testing of this technique as a tool for population augmentation (Faircloth et al. 2005). Strategically releasing captive-reared bobwhite chicks with known wild broods nearby or with potential adoptive wild parents using radio-telemetry may increase survival and warrants further investigation.

MANAGEMENT IMPLICATIONS

Our attempts to release chicks at different ages only minimally improved survival of adoptive parent-reared birds. However, the release of older individuals (10–12 weeks of age) may offer distinct survival advantages not observed in our study. Quality habitat existed on our study site suggesting that other factors are linked to the low survival of adoptive parent-reared chicks post-release. We do not recommend the release of PRAP bobwhites <9 weeks old as a bobwhite restoration tool. We recommend those interested in releasing adoptive parent-reared bobwhites to establish or augment current populations increase the number of birds released (>1 bird per acre of release area) to offset the low survival rates that we observed, especially in the first few weeks after release. The refinement of this technique to incorporate behavioral conditioning may increase survival rates of adoptive parent-reared birds after release by improving threat recognition and response. The cost to produce the number of chicks necessary for population recovery likely does not outweigh the return in the number of birds contributing to population viability—resources should be focused on wild bobwhite management.

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TESTING NORTHERN BOBWHITE REINTRODUCTION TECHNIQUES IN THE NORTHERN EDGE OF THEIR RANGE

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ABSTRACT

Pen-rearing young frequently fails as a reintroduction technique in game birds because of low postrelease survival rates in the wild. This may be caused by a combination of poor genetics from domestication, unhealthy birds, birds that do not exhibit wild behavior, or birds that are unfamiliar with their surroundings after hard releases. Recent research suggests that parent-rearing, involving pre- and posthatch imprinting of wild-strain northern bobwhite (*Colinus virginianus*) chicks by adults, may be a viable option for restoring populations. Imprinting potentially causes reintroduced birds to exhibit more natural behavior. We tested this method against a slightly modified traditional propagation tool (Surrogator®) with wild-strain birds. We conducted our research on a 170-ha property containing a mixture of early successional and hardwood habitat on Long Island, New York, during the summers of 2013 and 2014. We tested the effect of rearing methodology, mass at release (as a proxy for physical condition), release timing, and year on survival using Cox proportional hazard models. Hazard analysis revealed that only earlier release dates directly improved survival whereas treatment (parent-reared vs. Surrogator), body mass at release, and year did not affect survival. The methods tested on our study area did not result in 365-day survival rates high enough to re-establish quail in the area.

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Key words: Cox proportional hazards, foster parent, Long Island, New York, northern bobwhite, reintroduction, Surrogator, survival

The northern bobwhite (*Colinus virginianus;* hereafter, bobwhite) is a widely distributed gamebird in eastern North America but has experienced range contractions and precipitous range-wide declines in abundance since the 1960s (Sauer et al. 2014). Historically, bobwhites were found in early successional habitats ranging as far north as Ontario, Canada (Cadman et al. 1987); however, populations at the northern end of the species' range, including those in the Mid-Atlantic, have experienced particularly serious declines in abundance and distribution. Indeed, the northern populations in New York and New Jersey have been extirpated.

Bobwhites are near extirpation at the northern periphery of their range, so it is reasonable to employ endangered species restoration techniques. Endangered species management includes integrated strategies of habitat preservation, habitat restoration, and active management; however, Foin et al. (1998) found that 63% of endangered species would require more active management through initial habitat and population restoration or continued supplementation. Releasing captive-reared birds is one common active management strategy. Many captive breeding programs fail to reestablish wild populations (Beck et al. 1994), especially due to problems with 1) establishing self-sustaining captive populations, 2) poor success in reintroductions, 3) high costs, 4) loss of genetic variability due to domestication, 5) preemption of other recovery techniques, 6) disease outbreaks, and 7) maintaining administrative continuity (Snyder et al. 1996). However, in some cases, captive-breeding reintroduction programs have proven to be successful (e.g., California condor [*Gymnogyps californianus*] and black footed ferret [*Mustela nigripes*], Snyder and Snyder 1989, Jones et al. 1995). Therefore, to incorporate captive-breeding reintroduction programs, careful field studies that examine habitat suitability, genetics, physiological condition, site familiarity, and behavior must be conducted to provide measurable long-term success before their implementation (Snyder et al. 1996).

Physiological condition is important for successful reintroduction programs. Being transferred from one place to another, whether from one wild population to a new area or from captivity to the wild, puts stress on animals (Groombridge et al. 2004, Calvete et al. 2005,

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Franceschini et al. 2008) causing immune system suppression, leading to increased disease susceptibility, reduced reproductive capacity, and diminished fight–flight response, which could lead to increased predation (Dickens et al. 2009). Release methodology is also important for improving the chances of survival after release. Soft releases gradually introduce animals to the wild, often by releasing them into an on-site enclosure with shelter and food for a period of time in an effort to improve survival rates (Kleiman 1989). Using a soft release method may provide the animals time to safely learn about the environment (e.g., what type of food is available, what predators are on the landscape) without the actual hazards associated with being fully in the wild (Bright and Morris 1994, Mitchell et al. 2011). Hard releases, where animals are released directly into the wild without any acclimation in a contained environment or other support, can unnecessarily stress animals. A well-planned captive breeding program will carefully consider the implications of each of these factors to offer released animals the highest probability of survival.

A number of management strategies have been tested to reestablish northern bobwhites in areas of suitable habitat, including release of pen-reared bobwhites and translocation of wild bobwhites (Roseberry et al. 1987, Terhune et al. 2010). Attempts to restore bobwhite populations in suitable habitat using game-farm or pen-reared quail have been made since the early 1900s and continue into the present (Handley 1938, Wilson 1986, Perez et al. 2002). Propagation of game birds in captivity has long been regarded as a "quick fix" for better hunting (Hart and Mitchell 1947) and has been well-documented during the 1930s and 1940s (McAtee 1930, Hart and Mitchell 1947). However, this method of replenishing quail populations has proven unsuccessful for establishing sustainable populations. Pen-raised bobwhites often exhibit low rates of postrelease survival, averaging 8–15 days (Roseberry et al. 1987, Perez et al. 2002) and long-distance dispersal from release sites (Baumgartner 1944, Buechner 1950, Oakley et al. 2002). Additionally, pen-reared bobwhites that are released and survive until the following nesting seasons have been found to readily nest (DeVos and Speake 1995, Eggert et al. 2009) but they tend to have poor parenting skills and therefore low recruitment of young (Cass 2009, Eggert et al. 2009).

In response to historical problems associated with failed attempts of using pen-reared individuals to restore populations and the difficulty of obtaining wild birds for translocation, Wildlife Management Technologies (WMT; Wichita, KS, USA) developed a soft release methodology for pen-reared birds called "The Surrogator." The Surrogator® is a game bird propagation tool that provides food, water, heat, and shelter for incubator-raised chicks from day one through the first 5 weeks of life. Wildlife Management Technologies asserted that 300,000 quail were released from the Surrogator in 2006 with a subsequent survival rate from release to autumn harvest season of 0.65 (WMT 2009). However, recent multistate research failed to reproduce these results. Bobwhites reared in the Surrogator in Kansas had survival rates of 0.35 through 8 weeks and long-term survival was nil (Kinsey et al. 2012, Thackston et al. 2012).

As an alternative to releasing pen-reared birds, translocation of wild birds is the preferred and proven method to restore populations in suitable habitat. Translocation eliminates the behavioral and genetic problems associated with captive breeding programs, thus producing survival rates, nest production, and nest survival that are comparable to wild resident bobwhites (Terhune 2008, Terhune et al. 2010). However, translocation of wild bobwhites is often not an option because of legal (i.e., state restrictions to release birds to other states) and financial restrictions preventing the removal of wild birds from their current range (Hernández and Perez 2007).

In an attempt to combine the advantages of wild translocation along with the logistical ease of captive breeding, Palmer et al. (2012) developed a parent-rearing method for bobwhites that includes prenatal and postnatal learning with wild-strain bobwhites in group sizes that were similar to brood sizes. Bobwhite eggs removed from wild nests and hatched from incubators produced the breeding stock for the wild-strain bobwhites. This rearing method addresses the genetic and behavioral concerns of typical captive-rearing programs. In the past, some captive-rearing programs have been able to reduce behavioral limitations by using conspecific foster parents (Wiley et al. 1992, Snyder et al. 1996). Filial imprinting is an early form of learning during short prenatal (Lickliter 1989, 2005) and posthatch periods in which the chicks learn to identify their parents (Jaynes 1956, Hess 1973). Avian imprinting facilitates behaviors that enhance survival of offspring through sexual identification, social learning, predator recognition, predator avoidance, recognition of alarm calls, food selection, and parenting skills (Hess 1973, Dowell 1992, Lickliter and Harshaw 2010). Palmer et al.'s (2012) research on incorporating parent-rearing of wild-strain chicks found that nest success and chick survival were similar between parent-reared birds and wild birds, indicating that this method may be a successful alternative to the Surrogator for population restoration. However, Palmer et al.'s (2012) work was conducted in southern Georgia and South Carolina, where populations are more robust than those at the periphery of the bobwhite range. We do not know if parent-rearing can achieve similar levels of success at the edge of the bobwhite's range where density-independent stochasticity may introduce a complicating factor.

We tested these captive-rearing techniques on the bobwhite range periphery of Long Island, New York, where the bobwhite population is at or near extirpation. This research is intended to fill knowledge gaps in the area of bobwhite restoration techniques in northeastern/Mid-Atlantic states (Castelli et al. 2009); captive-bred bobwhites could be a valuable tool for preventing population collapse after major weather events in these peripheral populations. Our study was conducted with 3 main objectives. Our first objective was to test the effect of parent-rearing on bobwhites compared with those reared without parents (Surrogator). If parent-reared birds experienced higher survival rates, the results would point

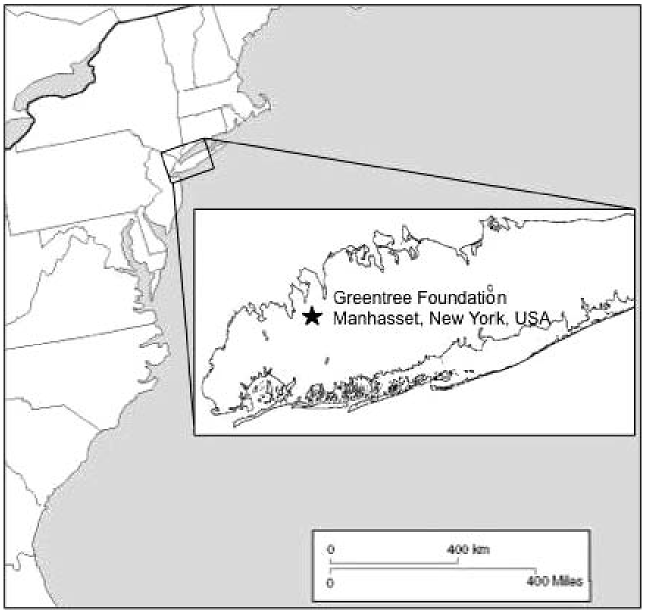

Fig. 1. Location of Greentree Foundation Property on Long Island, New York, USA, where we examined effects on postrelease survival of imprinting captive-reared northern bobwhite chicks on parental birds during 2013-2015.

toward the importance of imprinting (i.e., natural behavior) for successful bobwhite reintroduction efforts. Second, we examined the effect of body mass at release date as a proxy for the effect of physiological condition on postrelease survival. We assumed that individuals with a higher body mass at time of release were in better physiological condition than individuals with a lower body mass. Finally, we examined the effect of release date on daily survival rates. We did not examine the effects of habitat suitability or site familiarity because all of the bobwhites were released with a soft release methodology into the same habitat.

STUDY AREA

We conducted our research during May–December of 2013 and 2014 at the Greentree Foundation, a 170-ha area in western Long Island, New York, USA (Fig. 1). Approximately half of the property consists of dense hardwood forest comprising mostly oak (*Quercus* spp.), American beech (*Fagus grandifolia*), and maple (*Acer* spp.) trees. Dense understory in the woodland area provided ample bobwhite escape cover. The remainder of the property consists of early successional and grassland habitat and facility buildings. Areas of nonnative turf grass were gradually being replaced with native grass and forb mixes including species such as Indian grass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), and partridge pea (*Chamaecrista fasciculata*). Native grass and forb plantings provided nesting and foraging habitat. Food availability was supplemented with 2 food plot areas on opposite ends of the property consisting of mainly grain sorghum and proso millet. The predator community on the study area included feral cats (*Felis catus*), red foxes (*Vulpes vulpes*), great horned owls (*Bubo virginianus*), and various *Accipiter* and *Buteo* species. The annual mean temperature at the Greentree Foundation during 1981–2010 was 12.4° C with 118.3 cm of precipitation. The mean summer temperature was 22.9° C with 30.4 cm of precipitation. Mean winter temperatures were 1.8° C with 26.6 cm of precipitation (60.5 cm of snow; NOAA 2015). The mean summer temperature at Greentree was 22.6° C in 2013 and 22.8° C in 2014 with 32.9 cm of precipitation in 2013 and 29.6 cm in 2014. The mean winter temperature was 2.1° C in 2013 with 30.7 cm of precipitation and 0.74° C in 2014 with 36.7 cm of precipitation. The Greentree Foundation began raising bobwhites from domestic stock in the Surrogator for release on the property in 2011 (M. Afonso, Greentree Foundation, personal communication). Overwinter survival of these bobwhites was low and none of the birds released prior to the study were documented to have successfully reproduced.

METHODS

General Methods

In order to assess the impact of imprinting and physiological condition on survival of pen-reared bobwhites, we performed 3 trials during June, July, and September each year for 2 years using 2 Surrogators and 2 outdoor rearing pens placed at different locations on the property (<1.5 km apart) in areas considered to be suitable bobwhite habitat. We obtained "wild-strain" eggs from Quail Call Farms in Beachton, Florida, USA, although we could not definitively test the accuracy of their product. We placed eggs in 2 GQF Digital Sportsman (Savannah, GA, USA) cabinet-style incubators for 23 days at the start of each trial. We maintained the incubators at 37.5° C and 60% humidity for the first 20 days of incubation. We raised the temperature to approximately 37.8° C with a humidity of 75% for the last 3 days of incubation and while chicks were hatching. We divided "wild-strain" chicks hatched from one incubator between 2 separate Surrogators at 1 day of age. "Wild-strain" chicks hatched in the other incubator were imprinted to adult bobwhites and we moved them to trapezoidal outdoor rearing pens (4.9 m long, 2 m wide, and 2.84 m tall on one end, and 1.82 m high on the other end) within 48 hours of hatching.

Nonparent Rearing Methods

We used the 2 Surrogators already established on the Greentree property since 2011. We removed all vegetation and leaf litter from the immediate surrounding area for ease of maintenance. The Surrogators were set up and maintained according to all guidelines provided by the "Surrogator System Guide" (WMT 2009). During the 5-week period between hatching and release. The only contact chicks had with humans was during weekly maintenance of the Surrogator and when removing daily mortalities.

Chicks received commercial gamebird starter feed (Purina, St. Louis, MO, USA) with freestanding waterers. A wild-bird seed mix (consisting of proso millet [*Panicum miliaceum*], grain sorghum [*Sorghum bicolor*], cracked corn [*Zea mays*], wheat [*Triticum* spp.], and black oil sunflower seeds [*Helianthus annuus*]) was mixed into the commercial feed when the chicks reached 3 weeks of age. We gradually reduced brooder heaters from 21 to 35 days of age to prepare chicks for ambient temperatures upon release.

Chicks received a color leg-band (corresponding to the treatment type; i.e., Surrogator vs. parent-reared) and a uniquely numbered metal leg-band for future identification at 5 weeks of age. A randomly selected subset of juveniles from the Surrogators were fitted with a 3-g expanding radiotransmitter (American Wildlife Enterprises QC 300-day necklace transmitter, Monticello, FL, USA) before each release. We divided the bobwhites from each Surrogator into groups of approximately 5–20 to simulate a natural brood size (Stoddard 1931) before their release. We radiomarked 2–3 birds in each brood. We released each group approximately 30 minutes after sunrise at a unique site throughout the property. Release sites were reused for each trial.

Parent Rearing Methods

The Greentree Foundation constructed 2 sets of rearing pens housed 845 m apart in early successional habitat. Each set of rearing pens consisted of 4 pens adjacent to each another (Stoddard 1931). Each pen had a 1-m^2 shelter attached to its exterior where food was provided. A system of nipple waterers, similar to those used in the Surrogator, fed from a 5-gallon bucket of water was mounted to each pen. Sides and tops of the pens were covered in fine mesh wire fencing, allowing chicks to acclimate to local weather. The pens were enclosed by an electric fence to exclude mammalian predators after foxes depredated penned birds in summer 2014. Vegetation (e.g., grain sorghum, proso millet, etc.) was planted inside and outside of each pen to simulate natural brood habitat. We manually removed sod-forming grasses from the pens before each trial to facilitate movement throughout the pens by small chicks.

Bobwhite chicks were imprinted to adult foster birds and raised in outdoor pens following methods described by Palmer et al. (2012). Only domesticated bobwhites were available as a source for foster parents in the first year. However, in the second year, Quail Call Farms supplied "wild-strain" adults that had undergone the same imprinting process to be used as foster parents.

There was no supplemental heating provided for trials that took place from June through November. We retrofitted a heater from the Surrogator to the wooden box attached to the pens to provide supplemental heat for trials that started in December of 2013 and 2014. We fed chicks the same diet as for the Surrogator birds. The wild-bird seed mix was spread on the floor of the foster parent rearing pen instead of being mixed into the feeders for the Surrogator-reared birds. Spreading grain in the pen was intended to help prepare parent-reared chicks for foraging outside of the pens once they were released; this is not possible in the Surrogator because of its design. We expected insects to naturally enter the pens, allowing for additional protein and foraging training.

Juveniles received a color leg-band and a uniquely numbered metal leg-band for future identification and we fitted 2–3 birds from each brood with an expanding radiotransmitter after 5 weeks. Then, we released each group approximately 30 minutes after sunrise without the foster parent at a unique location on the study area near a similar sized nonparent-reared group. Parent-reared birds were released into areas of similar habitat as Surrogator birds but we released each treatment in a unique location. We released birds from each treatment near enough to each other that it was possible for birds from different treatments to encounter each other and interact because of the size of the study area. We used the same release locations for each trial.

We made 2 modifications to the original pen design after observing low survival rates in the pens for the first 2 trials. First, a 1-m-long, 2-m-wide, 0.5-m-high plexiglass "greenhouse" with a door to the rest of the pen and a roof that slid open was built in each pen. Chicks were held in these "greenhouses" for 2 weeks before the door to the rest of the pen was opened. This allowed the chicks to grow to a size that allowed them to thermoregulate more effectively before being fully exposed to the environment. When the door to the uncovered pen was opened, the lid to the greenhouse remained closed to provide a refuge from cold temperatures and precipitation. Instead of holding to a rigid release schedule of 5 weeks old, we waited to release the juveniles until the majority of the birds were $\geq$100 g; this was the minimum size where we could safely outfit the juveniles with radiocollars. Surrogator birds grew faster than parent-reared birds but they were held in the Surrogators until the parent-reared birds were ready for release to ensure consistency of treatments. Care, housing, and capture of bobwhites in this study was in compliance with requirements of the University of Delaware's Institutional Animal Care and Use Committee (#1242-2013-0).

Radiotelemetry

We used a telemetry receiver (Advanced Telemetry Systems Model R4000, Isanti, MN, USA) with a 3-element Yagi antenna to locate every bobwhite released via homing (White and Garrott 1990) to determine each individual's location. We tracked bobwhites 5–7 times/week until death between releases and the end of December to monitor survival. We monitored for survival once every other week between January and June. We used funnel traps (Stoddard 1931) and night-roost cast-netting (Brinkley 2011) to trap bobwhites that were released on the Greentree property beginning in June 2013 to supplement sample size of radiocollared bobwhites. We replaced transmitters in each group as mortalities occurred when we were able to capture uncollared birds. We identified recaptured birds to their treatment group and release date based on their uniquely numbered aluminum leg-band and corresponding color band. Over

Table 1. Sample sizes for northern bobwhite eggs incubated, hatched, and released in each trial of effects on postrelease survival of imprinting captive-reared chicks on parental birds, conducted during June 2013–December 2014 in Manhasset, New York, USA.

			Surrogator				Parent-rearing			
Initiation date	Hatch date	Release date	Eggs in ncubator	Chicks atched	Birds released	Radiocollared	Eggs in incubator	Chicks hatched	Birds released	Radiocollared
5 Jun 13	28 Jun 13	10 Aug 13	180	125	97	23	180	130	17	9
18 Jul 13	10 Aug 13	17 Sep 13	186	90	68	30	186	112	18	4
10 Sep 13	4 Oct 13	18 Dec 13	0	0	0	0	50	35	24	5
21 May 14	14 Jun 14	6 Aug 14	138	109	45	25	138	123	21	16
2 Jun 14	26 Jun 14	21 Sep 14	205	164	68	30	205	147	18	9
9 Sep 14	3 Oct 14	4 Dec 14	0	0	0	0	200	95	22	11
Total			709	488	278	108	959	642	120	54

the course of the study, we captured and radiocollared 17 Surrogator birds and 8 parent-raised birds.

Analyses

We used radiotelemetry data to estimate and compare survival rates between the treatments. The pulse rate of radiotransmitters doubled after they remained stationary for >18 hours. If a collar began to transmit a mortality signal, we located the collar and attempted to determine the cause of death for the bobwhite (Dumke and Pils 1973, Curtis et al. 1988). We pooled the data for all birds released from the Surrogators throughout the study and used a maximum likelihood estimator (Bart and Robson 1982) to calculate daily survival rates (Krebs 1999). In order to assess the effects of body mass and imprinting, we created Cox proportional hazard models (Cox 1972) using package Survival in R (Therneau and Grambsch 2000, Therneau 2015). We created 12 competing Cox proportional hazard models, including mass of birds at release, imprinting, trial (to account for effects of weather in different release months), and year effect. In order to avoid biasing the effect of trial on the models, we disregarded birds released in the third trial while creating our models because there were no Surrogator birds released in the third trial. We used Akaike's Information Criterion corrected for small sample size (AIC$_c$; Akaike 1976) to select the top survival model.

RESULTS

We incubated 709 eggs over 4 trials for the Surrogator treatment. We released 278 Surrogator juveniles total and fitted 108 with radiocollars. We incubated 959 eggs over 6 trials for the parent-rearing treatment. We released 120 parent-reared juveniles total and fitted 54 with radiocollars (Table 1; see Macaluso 2016 for details about each trial). The third trial of each year was dedicated to only parent-reared birds as an effort to improve sample sizes for survival analysis.

We pooled birds released from the Surrogators each year into one group to calculate maximum likelihood estimates of daily survival rates because of our small sample sizes. Daily survival rate of "wild-strain" chicks released on the Greentree Foundation was 0.95 (95% CI = 0.84–1.00), thus producing <0.001 cumulative survival rate after 105 days.

We compared Kaplan–Meier survival of radiocollared birds between parent-reared and Surrogator birds for the first 2 trials of each year without the examining potential interaction effects from other variables (e.g., year or mass; Fig. 2). We did not examine the survival curve for Trial 3 because there was no Surrogator group to compare with the parent-reared birds released in that trial. In 2013–2014, the survival rate 31 weeks after initial

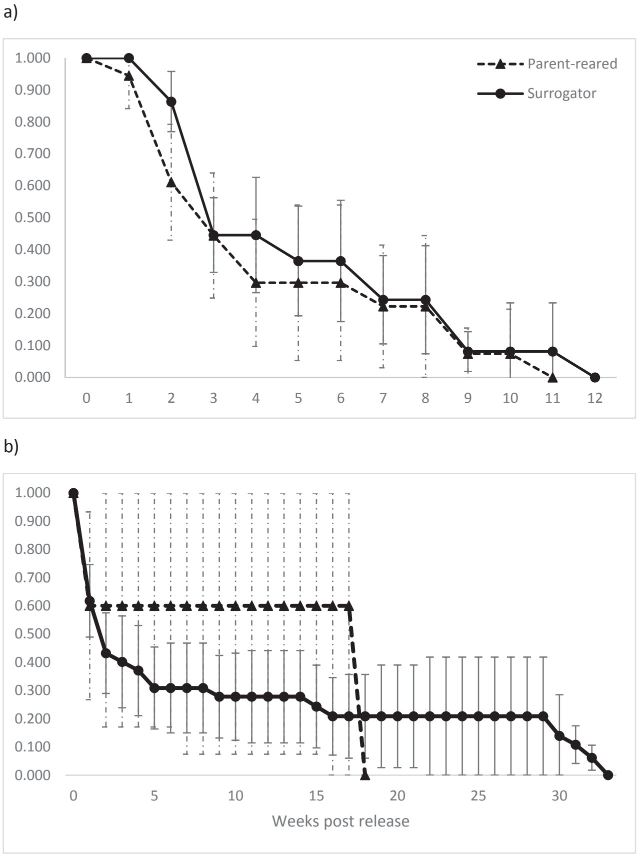

Fig. 2. Survival rates of radiocollared parent-reared and Surrogator northern bobwhite after release on the Greentree Foundation Property with 95% confidence intervals, Manhasset, New York, USA, comparing rates from birds released in the first (a) and second (b) trial per year, 2013–2015.

Table 2. Cox proportional hazards models comparing the effects of mass, imprinting, trial, and study year on survival rates of northern bobwhites released on the Greentree Foundation Property, New York, USA, 2013 and 2014. ΔAIC values <2.0 were considered to be the top competing models.

Model	K	AIC_c	ΔAIC_c	AIC_c wt	Cumulative wt
Null	1	507.63	0.00	0.288	0.288
Trial	2	508.30	0.66	0.206	0.494
Mass	2	509.51	1.87	0.113	0.607
Imprint	2	509.64	2.01	0.105	0.712
Mass + Trial	3	510.28	2.65	0.077	0.789
Imprint + Trial	3	510.37	2.73	0.073	0.862
Mass + Imprint	3	511.58	3.95	0.040	0.902
Trial × Year	4	511.89	4.25	0.034	0.936
Imprint + Trial + Mass	4	512.30	4.66	0.028	0.964
Imprint × Year	4	512.98	5.35	0.020	0.984
Imprint × Year + Trial	5	513.90	6.26	0.013	0.997
Imprint × Year + Trial + Mass	7	517.75	10.11	0.002	1.000

release (regardless of release date) was 0.123 for Surrogator birds and 0.0 for parent-reared birds. In 2014–2015, the survival rate 31 weeks after initial release (regardless of release date) was 0.033% for Surrogator birds and 0.0% for parent-reared birds. Despite the lack of long-term survival in both treatments regardless of trial date, birds from each treatment survived longer in the second trial.

The top Cox proportional hazard models ($\Delta AIC_c < 2$) included only imprinting, mass, and trial number as covariates; study year was not a covariate in any of the top models (Table 2). We used model-averaging within the R package AICcmodavg (Mazerolle 2015) to calculate model-averaged estimates of hazard covariates based on their slope coefficient for mass (0.00, 95% CI = –0.01–0.01), imprinting (0.29, 95% CI = –0.57–0.56), and trial (–0.6, 95% CI = –1.6–0.4) based on entire model set. All of the covariates for the model-averaged data had confidence intervals that included 0; therefore, none of the model-averaged covariates were significant either. Trial was the closest covariate to achieving significance and the trial-only model was the top performing model aside from the null model. Maximum likelihood estimates of daily survival rates decreased for both Surrogator and parent-reared bobwhites from Trial 1 through 3 (Fig. 3).

DISCUSSION

Lohr (2009) found wild bobwhites in New Jersey had a daily survival rate of 0.9934 and a cumulative October–March survival rate of 0.3. Population models for bobwhites in the Mid-Atlantic predicted that bobwhite populations need a daily survival rate of 0.9968 (winter survival rate of 0.561) to maintain a stable population (Williams et al. 2012). Although our reintroduction efforts did not produce a sustainable population, there are possible improvements to foster parent-rearing that might enhance probability of success or future attempts.

First, habitat suitability is considered the primary factor in any reintroduction study. We did not directly examine effects of habitat quality because birds were released in the same locations. Therefore, we acknowledge that our reintroduction into a fragmented northern landscape could have influenced the long-term success of quail reintroduction on Long Island. Nevertheless, our research design still allowed for a direct comparison of reintroduction techniques for future efforts.

Our estimated survival of “wild-strain” bobwhites raised in the Surrogators throughout the course of this study was 0.95. Although our rate is slightly higher than Kinsey et al.’s (2012) reported daily survival rates with domestic bobwhites raised in the Surrogators of 0.92, both studies exhibited survival rates that approached zero after 105 days. Our study did not provide evidence that improving the genetic makeup of bobwhites can significantly improve survival rates compared with the more traditional domestic birds. However, these results do not mean that genetics should be ignored when rearing bobwhites for reintroduction projects. Previous research with other species has proven that loss of genetic variability through domestication can negatively impact reintroduction efforts (Leopold 1944, Knoder 1959, Barbanera et al. 2010). Some might argue that “wild-strain” bobwhites used in this study came from Florida

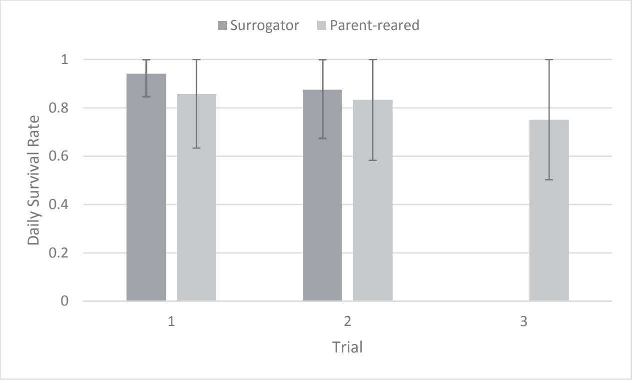

Fig. 3. Mean daily survival rates of radiocollared northern bobwhites after release on the Greentree Foundation Property with 95% confidence intervals, Manhasset, New York, USA, comparing rates between first, second, and third trial of 2013 and 2014.

and could therefore contain different genetics from those that a source population at a higher latitude source site would have. Although it would have been ideal to source the birds as near in location to the study area as possible, the reality is there was no other breeding program available to provide "wild-strain" bobwhite eggs. Furthermore, genetic studies of the current bobwhite population have shown little genetic variability between populations at different latitudes within the United States (Ellsworth et al. 1989, Wehland 2006).

Variation in body mass did not affect survival probability in this study. Previous research has tied body mass to survival of northern bobwhites (Buckley et al. 2015), but there may be other metrics to consider when assessing the effect of physiology on survival. For example, stress hormones could be collected from fecal samples to measure an index of stress for comparisons with survival rates (Rothschild et al. 2008). Birds that survived longer may have been in better physical condition than their brood mates; metrics other than mass might have been able to reveal this correlation.

Although imprinting was a variable in our top models, it was not a significant covariate in any of the models. Imprinting has been proven to have powerful behavioral consequences in other bird species (Hess 1973, Dowell 1992, Lickliter and Harshaw 2010) and has improved survival, predator avoidance, and reproduction for species other than bobwhites (Brittas et al. 1992, Dowell 1992, Buner and Schaub 2008, Gaudioso et al. 2011). Previous research showed that imprinting produced survival rates and reproductive success similar to those of wild bobwhites (Palmer et al. 2012). It is difficult to explain the discrepancy between this study and past reintroduction efforts that incorporated imprinting. There could be a latitudinal or other geographic effect on survival of using the parent-rearing methods. Further studies at latitudes between the 2 studies or in areas closer to or within the current bobwhite range would help determine the strength of these effects. Additionally, Palmer et al. (2012) speculated that the high survival rates of parent-reared bobwhites in their study might have been partially attributable to the wild bobwhites that already existed on their study area adopting the chicks post-release.

Daily survival decreased from Trial 1 through Trial 3. This suggests that bobwhites that are released later in the season face greater hazards compared with birds that are released earlier in the season. Weather can play a large role in the survival of bobwhites (Stoddard 1931); it stands to reason that releasing birds earlier in the season gives them time to acclimate to the landscape before winter comes. Admittedly, our early release dates may have been late compared with natural conditions, and our third trial was well outside typical fledging times for wild bobwhites. However, when one considers the timing of availability and limited supply of wild-strain eggs, our release dates are not outside a typical timeline for reintroduction efforts in our area.

Despite our best efforts to improve the rearing and release methods from the first year of the study to the next, there was no effect of year on survival of bobwhites in our study, although Cox proportional hazard rates were slightly higher in the second year of the study. It is difficult to determine why survival might have been lower in the second year compared with the first. It is possible that predation rates were higher because of an increased prevalence of predators on the study area. Predators may have developed a "search image" for quail or learned that prey was plentiful in the area because bobwhites were consistently being released there. This could have caused some predators to increase hunting efforts within the study area. Kinsey et al. (2012) found a positive relationship between dispersal distance and survival duration. A larger study area would have allowed the released birds to avoid predation by dispersing further from the release site. Alternatively, we could have varied the release sites more to avoid teaching the predators where their prey was likely to be. Weather might have also negatively affected survival more strongly in the second year of the study. Mean precipitation rates were below average during August–September and above average during October–December 2014. The lack of precipitation in late summer may have decreased available forage in 2014 while increased precipitation in the autumn and winter may have introduced extra stress to the birds, causing them to allocate more energy toward thermoregulation in the rain and snow.

MANAGEMENT IMPLICATIONS

Our research revealed that timing of release is one of the most important factors to consider when planning a bobwhite reintroduction effort. Future reintroduction efforts should not only build upon our methodology but expand it to multiple sites to reveal habitat effects on postrelease survival or to use experimental releases to identify potential source habitats. Although imprinting was shown to improve success rates in other studies, it did not have a significant impact on survival in our study system. Body mass did not contribute to the hazards experienced by bobwhites, so it would be worth experimenting with releasing birds at younger ages. Wild adult bobwhites stop caring for their chicks after approximately 2 weeks (Rosene 1969). Releasing chicks at a younger age would reduce the amount of time spent in captivity and could produce birds that behave more like their wild counterparts. Additionally, holding chicks for shorter periods of time would free up pen space faster, allowing more trials to take place early in the season when survival rates are higher. Future reintroduction efforts should strive to release birds early in the season, close to the average timing of bobwhite breeding, to ensure success. Survival of parent-reared birds was higher compared with Surrogator birds in the second year of our study (Fig. 2). This could have been due to improvements in learned behavior during the second year because foster parents were also parent-reared "wild-strain" birds compared with the domestic bobwhites used in the first year. Further research on the effect of foster parent source could prove interesting and valuable to future parent-reared introduction efforts.

ACKNOWLEDGMENTS

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PARENT-REARED BOBWHITE SURVIVAL IN THE TEXAS ROLLING PLAINS

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ABSTRACT

Considerable research has been accomplished over the past 6 decades on the possible reasons for decline in the northern bobwhite (*Colinus virginianus*), henceforth known as the bobwhite. Restoring or restocking bobwhite populations by augmentation in areas that once held significant numbers has been a focus for many wildlife agencies and managers. Three main methods for augmentation of bobwhites currently exist: release of pen-raised birds, release of juvenile birds reared by Surrogator®, and translocation of wild bobwhites from one area to another. Of these 3 methods, only translocation has accomplished the goal of reestablishing bobwhite populations. Recently a new model developed by Tall Timbers Research Station in Tallahassee, Florida, USA, has successfully produced parent-reared bobwhite chicks from wild strain, which are raised by a surrogate parent in a simulated wild habitat environment. These birds have been released into the southeastern United States and successfully established new bobwhite population in areas of restored habitat. We designed a study to determine the viability of this rearing and release method for restoring depleted bobwhite populations in the semiarid, Rolling Plains of Texas. One hundred fifty nine radiomarked, parent-reared bobwhites were released in 2013–2014 on 8 ranches. One hundred five radiomarked, parent-reared bobwhites were released in 2014–2015 on 6 ranches. The survival rates were low for both years of the study with only 4 radiomarked birds surviving the first year and no birds surviving the second year. An apparent lack of predator-avoidance skills appears to be responsible for the high mortality rates that we estimated.

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Key words: anti-predator behavior, *Colinus virginianus,* parent-reared bobwhites, population augmentation

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SUMMER SURVIVAL OF TRANSLOCATED NORTHERN BOBWHITE IN THE NEW JERSEY PINE BARRENS: PRELIMINARY RESULTS

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) have declined precipitously since the 1960s, largely due to habitat deterioration and changes in land use; some of the highest declines have been observed in the Mid-Atlantic States. In other regions, attempts to augment bobwhite populations have been relatively successful using translocation. As part of a long-term restocking program, focal areas for translocation in the mid-Atlantic region were identified by biologists at a National Bobwhite Conservation Initiative (NBCI) workshop. The objective of this project is to evaluate translocation to restore bobwhite populations in the New Jersey Pine Barrens, a focal area designated with a high ranking for potential bobwhite recovery. The study site, Pine Island Cranberry Co., is the largest privately owned land tract (>6,000 hectares) in New Jersey, with a mix of shortleaf pine (*Pinus echinata*), pitch pine (*P. rigida*), scrub oak (*Quercus ilicifolia*), and early successional forbes and grasses. For three consecutive years (2015—2017) prior to breeding season, we are translocating eighty radio-collared bobwhite (40 male, 40 female) from wild populations in southwest Georgia. These individuals are radio-located 3-5 times per week, year round. We are collecting microhabitat measurements (e.g., groundcover, understory, and canopy closure) and monitoring nests to characterize habitat use, nest site selection, and nest fate. Survival is estimated using staggered-entry Kaplan-Meier analyses and a Cox proportional hazard model in R to determine covariates of daily mortality. Six of 14 nests were successful in summer 2015 (66 known hatches), and 0 of 12 nests were successful in summer 2016. Snake depredation was the cause of 41.7% of failed nests in 2016. Preliminary analyses produce a five-month adult survival rate of 0.455 (SE = 0.138) for summer 2015 and 0.270 (SE = 0.0516) for 2016. Our planned third summer (2017) of data collection will increase our understanding of these disparate survival estimates.

Citation: Coppola, P. M., K. R. Stevens, C. K. Williams, T. M. Terhune, J. P. Parke, and J. Cecil. 2017. Summer survival of translocated northern bobwhite in the New Jersey Pine Barrens: Preliminary results. National Quail Symposium Proceedings 8:185.

Key words: *Colinus virginianus*, northern bobwhite, translocation, radio-telemetry, nesting, survival, habitat use, habitat management

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WINTER SURVIVAL AND HABITAT SELECTION BY TRANSLOCATED NORTHERN BOBWHITE IN THE NEW JERSEY PINE BARRENS: PRELIMINARY RESULTS

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) populations have been experiencing precipitous range-wide declines for more than 50 years; some of the steepest declines occurring in the Mid-Atlantic states. These declines are largely attributed to habitat deterioration from urban sprawl, change in forest management, and intensive farming. This ongoing study aims to evaluate the efficacy of translocating wild bobwhites into the New Jersey Pine Barrens as a means to restore their historic populations. Translocation has proven relatively successful in augmenting bobwhite populations in other regions as well as restoring populations of gallinaceous species. This portion of the study aims to investigate what bobwhites require during winter months (October—March) in the Mid-Atlantic to survive until summer for reproduction. The study site, Pine Island Cranberry Company, is the largest privately owned tract of land (6,800 hectares) in New Jersey, with habitat comprised of pitch pine (*Pinus rigida*), shortleaf pine (*Pinus echinata*), scrub oak (*Quercus ilicifolia*), and early successional forbs and grasses. For three consecutive years (2015—2017) prior to breeding season, we will translocate 80 radio-collared bobwhites (40 male, 40 female) to Pine Island from wild populations in southwest Georgia. These bobwhites are radio-located 3—5 times per week throughout the year while this portion of the study focuses on the winter months. We are collecting microhabitat measurements (e.g., basal density, groundcover, understory, and canopy closure) from 30 random telemetry location points, per covey, per habitat type to characterize winter habitat use. Survival is estimated using staggered-entry Kaplan-Meier analyses and a Cox proportional hazard model in R to determine covariates of daily mortality. We are reporting on the first 2 years of results.

Citation: Stevens, K. R., P. M. Coppola, C. K. Williams, T. M. Terhune, J. P. Parke, and J. Cecil. 2017. Winter survival and habitat selection by translocated northern bobwhite in the New Jersey Pine Barrens: preliminary results. National Quail Symposium Proceedings 8:186.

Key words: *Colinus virginianus*, northern bobwhite, translocation, radio-telemetry, survival, habitat use, habitat management, pine ecosystem

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EFFECTS OF SUPPLEMENTAL FEEDING ON BREEDING SEASON HOME RANGES AND RESOURCE SELECTION OF NORTHERN BOBWHITES

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ABSTRACT

Providing supplemental food resources for northern bobwhite (*Colinus virginanus*) has been a common management practice for decades, but its impact on bobwhite home ranges sizes and space use has been debated. Between 2001 and 2007, we established a 397 ha fed study area on Tall Timbers Research Station, which received grain sorghum biweekly along a 19.5 km feed trail. An adjacent 465 ha area was treated as a control with no supplemental food resources. Radio-tagged wild bobwhites were located 3 – 5 times each week throughout the breeding season and we used these locations to calculate home ranges during early breeding season (15 April – 30 June) and late breeding season (1 July – 1 October). We also determined second and third order selection of a 10-m buffer area surrounding the supplemental feed trail using compositional analyses. In total, 552 and 286 bobwhite home ranges were calculated for early and late breeding seasons, respectively. We observed significantly smaller early breeding season home ranges on the fed area ($\bar{x} = 12.3$ ha, 95% CL ± 0.6) relative to the control ($\bar{x} = 17.4$ ha ± 1.9). Average length of feed trail within home ranges was 583 m and 710 m for early and late breeding season home ranges, respectively. The feed trail buffer area was 3 to 5% of all home ranges. Home range placement was not random with high selection preference for the feed trail buffer area. However, there was a low selection preference for the feed trail buffer area within home ranges. Average distances to the feed trail for bobwhite locations ($\bar{x} = 64.4$ m ± 16.1) was similar to random locations ($\bar{x} = 74.4$ m ± 16.9). The effect of supplemental feeding on bobwhite home ranges size and resource use was greatest during the early breeding season when food and useable habitat were likely lower in availability. On our study area, supplemental food resources distributed along a feed trail impacted bobwhites during a critical transition period from the spring prescribed burning season to the early breeding season.

Citation: Wellendorf, S.D., W. E. Palmer and A. M. Bostick. 2017. Effects of supplemental feeding on breeding season home ranges and resource selection of northern bobwhites. National Quail Symposium Proceedings 8:187–195.

Key words: *Colinus virginanus*, Florida, home range, northern bobwhite, resource selection, supplemental feeding

INTRODUCTION

Providing supplemental food resources for northern bobwhites (*Colinus virginanus*) (hereafter: bobwhite or quail) has been a common management practice for many decades (Frye 1954, Guthery 1986, Sisson et al. 2000). Historically, stationary feeders have been used to provide a high energy grain such as sorghum (*Sorghum bicolor*, hereafter: milo), and/or corn (*Zea mays*) (Townsend et al. 1999, Doerr and Silvy 2002, DeMaso et al. 2002, Guthery et al. 2004). Concern exists that supplemental feeding may increase disease transmission, predation, and harvest, because bobwhites are attracted to a known point (Godbois et al 2004, The Wildlife Society 2006). More recently supplemental feeding with milo along a designated feed trail has become a widely-used management practice on quail hunting properties (Michener et al. 2000, Sisson et al. 2000, Haines et al. 2004, Buckley et al. 2015). Spreading grain along a continuous feed trail through suitable habitat may not concentrate bobwhites at a location, therefore alleviating these concerns; however research on the effects of a feed trail on home range size, placement, and resource selection is limited.

Initially, supplemental feeding was used during the nonbreeding season to provide high energy foods during winter months when declining food resources and severe weather reduced availability of native foods to bobwhites (Frye 1954, Robel and Slade 1965). As such, researchers have focused on effects of supplemental feeding on bobwhite nonbreeding season movements and home ranges (Sisson et al. 2000, Buckley et al. 2015, Miller et al. this volume). In southwest Georgia, Sisson et al. (2000) observed smaller nonbreeding season home ranges on a supplemental feed trail area compared to a nearby but separate control area and noted more localized move-

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ments and shorter foraging times on the fed area. Similar results were observed in south Texas with decreased home range size and localized movements around feed trails on a treatment area (Haines et al. 2004) when compared to control area. Conversely, Buckley et al. (2015) in the Rolling Plains of Texas and Miller et al. (this volume) in northern Florida observed no effect on home range size during the nonbreeding season from supplemental feeding.

Supplemental feeding during the breeding season may affect bobwhites differently than during the nonbreeding season. During the breeding season bobwhites have access to increased natural food availability, such as insects, fruits, and seeds. Further, habitat availability and the suitability of those habitats rapidly change during the breeding season, especially in pine savanna systems with frequent prescribed fire. After the application of prescribed burning during March – April, bobwhites use the previous year's habitat for cover and nesting until vegetation recovers in burned habitats, then increasingly use burned habitats for nesting and brooding during late summer (Stoddard 1931, Carver et al. 1998). The presence of a supplemental feed trail may affect bobwhites' home range size and spatial position, and how bobwhites allocate time in habitats within their home range, and these effects may be different in the early versus late breeding season.

Research on the impacts of supplemental feeding on bobwhite habitat and resource use during the breeding season is lacking. Therefore, the objectives of this research were to determine the impacts of a continuous supplemental feed trail during 2 time periods within the breeding season for the following variables: 1) home range size, 2) second and third order habitat and resource selection (Johnson 1980), and 3) location proximity to the feed trail. This research project was part of a larger experiment that investigated the impacts of supplemental feed on multiple bobwhite parameters, including survival and reproductive output during the breeding season; these data will be presented in a separate manuscript.

STUDY AREA

We conducted this study on Tall Timbers Research Station (TTRS) (1,568 ha), Leon County, Florida (30.66° N, 84.22° W). The landscape composition of TTRS was rolling hills consisting of primarily upland pine forests (66%) including loblolly pine (*Pinus taeda*), shortleaf pine (*Pinus echinata*), and longleaf pine (*Pinus palustris*) in the overstory, and equal proportions of grasses, forbs, and shrubs associated with "old-field" plant succession in the understory. Intermixed throughout the uplands were mesic hardwood-dominated drainages and wetlands (17%), annually disked fallow fields (13%) which were 0.4 to 1.2 ha in size, and open wet areas (4%). Prescribed fire was used throughout TTRS on a 2-year interval to control encroachment of hardwood trees and to maintain the mix of herbaceous and woody ground cover. Approximately, 50% of the uplands were burned each year between March and April in an alternating mosaic of patches ranging from 2 to 20 ha. Other management practices used were spot mowing and roller chopping of hardwood and pine saplings in recently burned upland areas to assist with hardwood control. In 2007, a selective timber harvest was completed on all upland portions of the study areas. Land management objectives were to optimize upland habitat suitability for bobwhites throughout the year.

Between January 2001 and December 2007, TTRS was divided into 2 approximately equal sides with 1 side receiving supplemental feed (hereafter: supplemental feed treatment area or fed area) that was 397 ha in size and the other side with no supplemental feed (hereafter: control area) was 465 ha. On the fed area, approximately 1,651 kg (2,290 liters) of milo seeds were scattered along a designated feed trail every 2 weeks, year around, throughout the upland pine forest and fallow field edges in areas useable by bobwhites (Figure 1). Supplemental feed was applied using a tractor with an attached broadcast spreader. The feed trail was established to maintain a consistent line density of 2.4 km of feed trail per 40.5 ha of useable habitat over the entire fed site, which summed to an overall feed trail length of 19.5 km. The overall rate of milo spread every two weeks was 84.6 kg of milo per each km of feed trail.

METHODS

Telemetry Data

For the years, 2001 – 2007, bobwhites were captured in January and March using standard walk-in funnel traps (Stoddard 1931). We determined sex, age class, and weight for each captured bobwhite and attached a uniquely numbered aluminum leg band (National Band and Tag Co., Newport, KY 41072). From each captured covey we selected 2-3 bobwhites to be fitted with a 6-g radio transmitter (American Wildlife Enterprises, Monticello, FL 32344). Radio transmitters were distributed at an approximate ratio of 1 radio-tagged male to 4 radio-tagged females. In January, trapping efforts and radio distributions were equally applied to all areas of TTRS, while March trapping was focused on areas with an inadequate radio tag sample. Trapping, handling, and marking procedures were consistent with Palmer and Wellendorf (2007) and followed the guidelines of the Tall Timbers Research, Inc. Institutional Animal Care and Use Committee Permit (#GB2001-01).

For all years, radio-tagged bobwhites were located 1 to 3 times weekly until 15 April and then 3-5 times weekly thereafter until 1 October. We determined locations of radio-tagged individuals using homing procedures (White and Garrott 1990) and then marked locations on detailed landcover maps developed in ArcGIS (ESRI, Redlands, CA). While the precision of calculated locations to the actual locations of radio-tagged bobwhites has not been formally determined, we thoroughly trained technicians on the homing technique to ensure they determined locations to within at least a 10 m^2 area. Additionally, they verified that the correct macrohabitat landcover type (e.g., burned upland, unburned

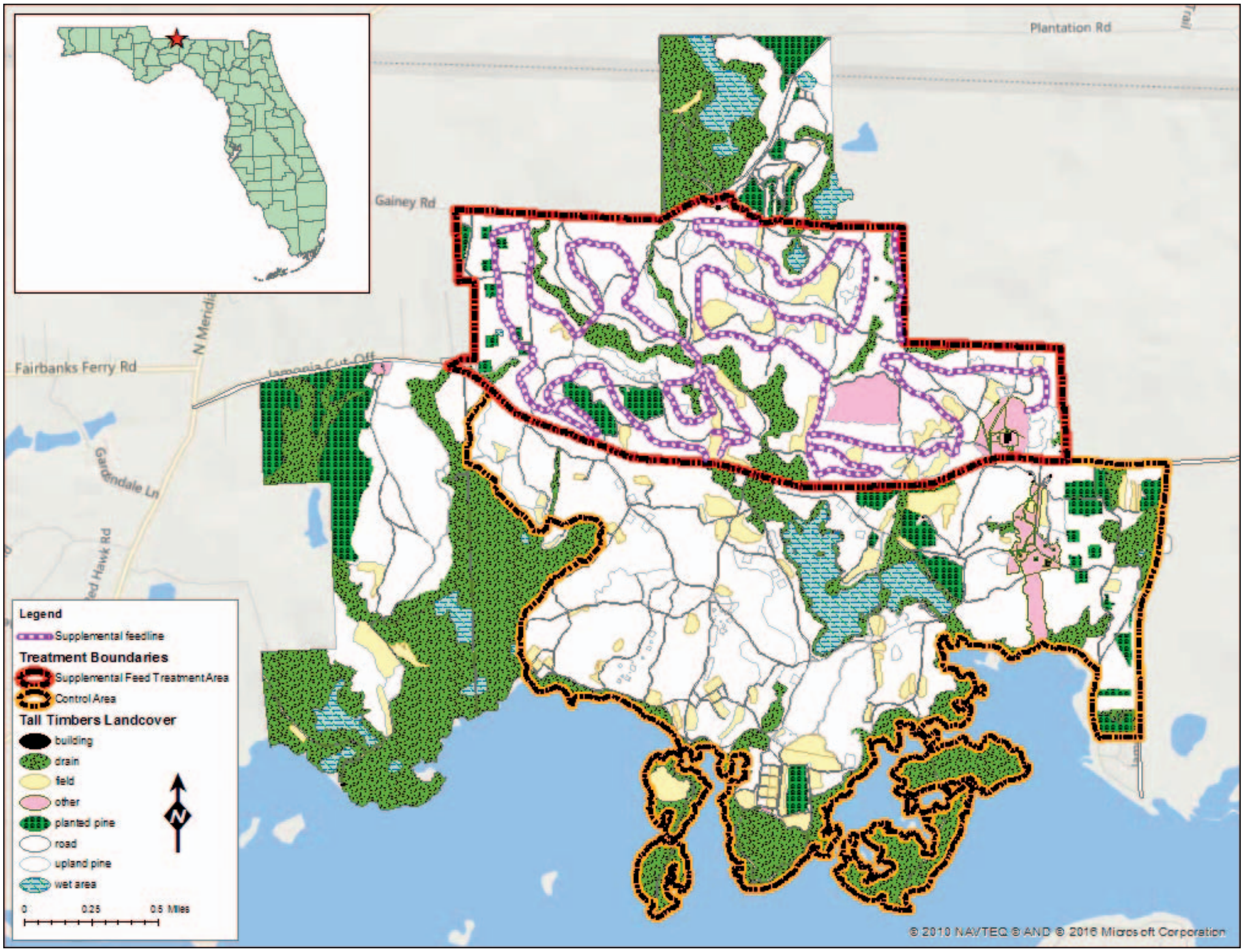

Fig. 1. A map of the supplemental feed treatment area with the feed trail and the control area on Tall Timbers Research Station and Land Conservancy, Leon County, FL, USA.

upland, field, hardwood drain) or feed trail was assigned to the location. Transmitters motionless for 12 hours changed pulse rate to notify observers of a potential mortality. Idle transmitters were located to determine if mortality or transmitter slip had occurred.

We determined that a bobwhite was nesting when its locations were unchanged for 2 consecutive days and the mortality sensor had not activated. Nesting sites were flagged and monitored daily until a depredation or hatch. Bobwhites with a hatch were treated as a brood until 14 days post hatch or until it was determined the bobwhite was no longer with a brood.

Data Analysis

Within the reproductive season, we calculated bobwhite home ranges and resource use at 2 specific time intervals (Taylor and Burger 2000). The early breeding season, 15 April – 30 June, was meant to capture the period of post covey dispersal, pre-incubation activity, first incubated nesting attempts, and early brood rearing activities. The late breeding season, 1 July – 1 October, corresponds to all reproductive activities and pre-covey development.

In order to minimize any potential bias of repeated observations at the nest site on home range size or resource selection, only 1 nest site location for each nesting attempt was used in the analysis. Since bobwhites were only located once per day, incubating birds were typically located on the nest. These repeated locations during the incubation period would have potentially resulted in a compacted home range and resource selection concentrated around the nest site, and therefore repeated locations were removed. We did include all brood locations in the analysis.

Home Range Calculations

For every breeding season, each bobwhite location was determined to be in one of the following areas: supplemental feed treatment area, control area, other TTRS areas, or off property. For each bobwhite, in each breeding season, we calculated the percentage of total locations for each of the areas. We assigned a treatment type to a bobwhite when more than 75% of their locations were observed within an area. This is an arbitrary classification meant to assist with assigning a treatment type based on the majority of locations, but allow for some individual bobwhite locations to be outside of the treatment boundary. Prior to any home range or resource use analyses, we determined the average percentage of locations for bobwhite classified in the supplemental feed treatment and control areas. Over the 6 years, birds assigned the supplemental feed treatment had an average of 96% of bobwhite locations within the supplemental feed treatment area. For the control area, 95% of locations were in the control area for birds assigned to the control area.

Home ranges were only calculated for bobwhites that survived the entire period of interest, which was done to minimize any potential bias to home range size due to reduced sample size because of any possible survival differences between treatment areas. For each surviving bobwhite we computed a fixed-kernel home range using a bivarate normal (Gaussian) kernel density estimator (HRT: Home Range Tools for ArcGIS; version 1.1; Rogers et al. 2007) in ArcGIS 9.3. Prior to home range estimation, the bandwidth (*h*) was calculated for all individuals using a least-squares cross-validation procedure (LSCV) for each time period (adehabitat package, https://www.faunalia.it/animove/trac/; R Foundation for Statistical Computing, Vienna, Austria) (Calenge 2006). Home ranges that did not converge were removed from any further analysis. We estimated the median h_{lscv} value for all remaining home ranges for each time period and this value was used as the bandwidth value for all home range calculations (Kenward 2001). For the raster portion of the kernel home range procedure we used a grid cell size of 10 m, which we estimated to be an appropriate scale for bobwhites, considering location resolution. From the grid that was produced we calculated a 95% volume contour, which was used in the comparison between the control and supplemental feed treatment areas.

Resource Use

We describe habitat and resource use for the supplemental feed treatment area only at 2 spatial scales, corresponding to Johnson (1980), second and third order selection using compositional analysis (Aebischer et al. 1993, Martin et al. 2013). Our primary interest was in the selection preference of the feed trail buffer area relative to other habitats on the fed area.

At the beginning of the breeding season each year we mapped macro-habitat classifications for the supplemental feed treatment area. Annual evaluation was necessary due to changes from prescribed fire applications and minor adjustments to the feed trail made each year. Macro-habitat classifications used in the analysis included: feed trail buffer area, burned upland pine, unburned upland pine, annually-disked weed fields (field), and forested hardwood mesic drainages and wetlands (drain). In order to develop an area for the linear feed trail a 5 meter buffer was applied to each side (10 m total width) to represent the area where supplemental feed was applied. The proportional area of the supplemental feed trail buffer area ranged between 2.7 and 3.1% of the treatment area. For each home range, the proportional amount of each macro-habitat was determined. We determined amount of available habitat for the second order resource selection analysis by calculating a minimum convex polygon (MCP) around all points used for each year and time interval combination. Each year/season MCP was expanded by a 100 meter buffer to account for habitat influences beyond the MCP. Proportional habitat and feed trail buffer area amounts were compared to habitat proportions within the supplemental feed treatment area for each year and both time intervals to determine second order resource selection. For third order resource selection, we calculated the proportional use by determining the macro-habitat for each bobwhite location within each home range and compared those values to the proportional habitat amounts available within each bobwhite's home range. Similar to Taylor and Burger (2000) and Martin et al. (2013), we used a multivariate approach to test if resource use of bobwhite were at random for second and third order selection. We used the adehabitat package (Calenge 2006) for program R to conduct the analysis according to Aebischer et al. (1993). Prior to analysis, we replaced zero values for use with the value 0.001 which was one order of magnitude less than the smallest recorded nonzero proportion (Aebischer et al. 1993).

Proximity to Feed Trail

We wanted to determine if bobwhite locations were closer in proximity to the feed trail relative to random locations within the feed trail treatment area at both breeding season time intervals. Random points were calculated within each home range using Geospatial Modeling Environment software (version 7.4.0, www.spatialecology.com, 2009-2015), and random numbers were equal to bobwhite locations used to produce the home range. For each year, distance to the feed trail for all random and bobwhite locations were calculated using the near function in ArcGIS (version 10.3 ESRI, 2015).

RESULTS

Early Breeding Season Home Range

We calculated early-breeding season home ranges for 554 radio-tagged bobwhites for the years 2001 – 2007, of which 2 home ranges did not converge and those observations were removed from any additional analysis. The median h_{lscv} was 30.1 and this value was used as the smoothing parameter for all early-breeding season home ranges. There were 27,205 locations used in the analysis with an overall mean of 49.2 (SD = 22.1) locations per radio-tagged bobwhite. Early breeding season home ranges for the fed areas were similar among years (CV = 7.1%), and ranged from 11.6 ha to 14.1 ha with an overall average of 12.3 ha (95% CL = 0.64) (Table 1). For control areas, early season home ranges fluctuated between 14.8 ha and 21.5 ha, averaged 17.4 ha (95% CL = 1.89), and had higher variability among years (CV =

Table 1. Average home range size of northern bobwhites on supplemental feed treatment areas and control areas for Tall Timbers Research Station, Florida, USA.

		Early-Breeding Season Home Range			Late-Breeding Season Home Range		
Year	Treatment	*n*	$\bar{x}$	95%CI	*n*	$\bar{x}$	95%CI
2001	Fed	12	14.1	2.3	4	15.7	3.3
	Control	57	21.5	1.7	25	19.9	3.2
2002	Fed	39	11.7	1.1	30	14.8	1.5
	Control	117	15.8	0.9	68	15.7	1.3
2003	Fed	23	12.7	1.5	7	16.7	2.7
	Control	49	16.0	1.4	25	19.6	2.1
2004	Fed	31	11.6	1.3	11	13.5	2.2
	Control	25	18.8	2.2	9	20.6	5.4
2005	Fed	29	12.0	0.9	13	14.7	1.6
	Control	34	15.2	1.3	16	19.4	2.1
2006	Fed	44	11.8	1.1	24	14.3	1.4
	Control	42	14.8	1.0	25	18.6	2.4
2007	Fed	28	12.3	1.1	19	15.2	1.9
	Control	22	19.5	2.6	7	21.5	4.4

14.7%). Annual early breeding season home ranges were between 20.3% and 36.9% smaller on fed areas than control areas (Figure 2). For the fed area, every calculated home range had a portion of feed trail within its area. The feed trail lengths ranged between 36.4 and 1,631.0 m with an overall mean of 582.9 m (SE = 18.0, n = 171).

Late Breeding Season Home Range

We calculated late breeding season home ranges for 286 radio-tagged bobwhites for 2001 – 2007. There were 15,389 bobwhite locations used in the analysis with an overall mean of 53.8 (SD = 15.9) locations per radio-tagged bobwhite. The smoothing parameter was a median h_{lscv} of 32.9, and all late breeding season home ranges converged. Late season home ranges for the fed areas pooled for all years was a mean of 14.9 ha (95% CL = 0.76) with minimal annual variability (CV = 6.8%). On control areas, we observed larger late season home ranges that averaged 19.3 ha (95% CL = 1.37) among years and were also relatively consistent (CV = 9.5%). The late season home ranges on fed areas were between 5.7% and 34.5% smaller than control area home ranges (Table 1). Every late breeding season home range in the supplemental feed treatment area had at a portion of feed trail within the calculated area. Feed trail lengths ranged between 136.5 and 1,433 m with an overall mean of 710 m (SE = 26.5, n = 96).

Habitat and Resource Use of Fed Areas

Early Breeding Season Resource Use.—We calculated second and third order habitat and resource selection for 175 early breeding season home ranges for all years, except 2004, which was excluded due to missing landcover data. There was a nonrandom use of resources in the positioning of home ranges and within home ranges among all years ($0.1221 \leq \Lambda \leq 0.459$, $P < 0.05$). We observed that bobwhites oriented home ranges with a selection preference for the feed trail buffer area as compared to other habitats in the surrounding study area, and the feed trail buffer area had the highest or second highest rank for all years (Table 2). This selection preference for the feed trail buffer area was significant relative to all other habitats in 2002 and 2005. In 2006 and 2007, there was a significant selection preference for the

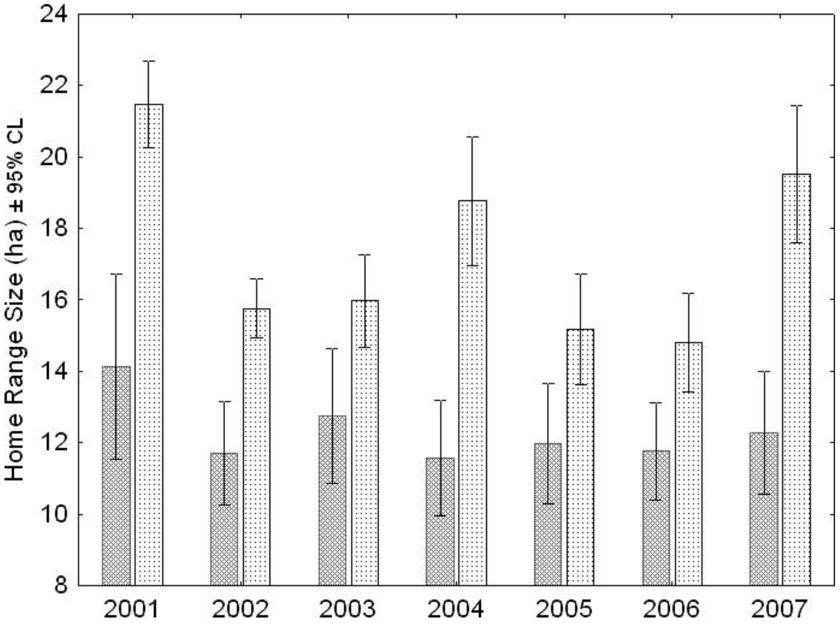

Fig. 2. Comparison of average early breeding season home ranges of northern bobwhites for supplemental feed treatment and control areas, Leon County, FL, USA, April – October, 2001 – 2007. Dark gray bars represent the supplemental feed treatment area and light gray represent the control area.

Table 2. A compositional analysis simplified ranking of second order habitat and resource selection for northern bobwhite on the supplemental feed treatment area during the early breeding season, Tall Timbers Research Station and Land Conservancy, 2001 – 2007.

YEAR	*n*	Habitat Rank 5[a]	[b]	Habitat Rank 4		Habitat Rank 3		Habitat Rank 2		Habitat Rank 1
2001	12	feed trail buffer area	>	unburned upland pine	>	burned upland pine	>	field	>>>	drain
2002	39	feed trail buffer area	>>>	burned upland pine	>	unburned upland pine	>>>	field	>	drain
2003	23	unburned upland pine	>	feed trail buffer area	>	burned upland pine	>	field	>>>	drain
2005	29	feed trail buffer area	>>>	unburned upland pine	>	burned upland pine	>>>	field	>	drain
2006	44	unburned upland pine	>	feed trail buffer area	>>>	burned upland pine	>>>	field	>	drain
2007	28	unburned upland pine	>	feed trail buffer area	>>>	drain	>	burned upland pine	>	field

[a] An increase in rank value signifies increased use relative to the study area.

[b] The >>> symbol represents significant resource selection preference over lower ranked habitats, and the > symbol represents resource selection preference over lower ranked habitats.

feed trail buffer area and unburned upland pine compared to other habitats.

Within home ranges, we observed a significantly higher selection preference for unburned and burned upland pine habitat, which had the highest or second highest ranking for all years, when compared to the other habitats and feed trail buffer area (Table 3). Also, selection preferences for both upland pine habitats were significantly higher than the feed trail buffer area for 5 of 6 years.

Late Breeding Season Resource Selection.—For late season breeding home ranges we determined second order habitat and resource use selection preferences for 96 home ranges relative to the surrounding study area for 2002 – 2007. Habitat and resource selection preferences were not calculated for 2001 due to small sample size and 2004 due to missing landcover data. There was a nonrandom use of resources in the positioning of home ranges and within home ranges for all years ($0.0566 \leq \Lambda \leq 0.469$ $P < 0.05$), except in 2003, when we observed third order selection with no significant selection preference. For 2002, 2005 and 2006, the feed trail buffer area had a significantly higher selection preference relative to other habitats and was the highest ranked resource type (Table 4). In 2007, selection preferences were similar among feed trail buffer area, unburned upland pine, and fields, but the feed trail buffer area was the second ranked resource type.

Selection of the feed trail buffer area within home ranges, third order selection, for late season breeding home ranges was not significant compared to selection of resource types. The feed trail buffer area was ranked lower than burned and unburned upland pine for every year (Table 5).

Distance to Feed Trail.—For the early breeding season, the mean distances to the feed trail for bobwhite locations were less for all years when compared to random locations, with an overall mean distance of 67.4 m (± 15.6) and 76.5 m (± 15.7) for bobwhite and random locations, respectively (Table 6). Among years, bobwhite locations were between 4 and 21% closer to the feed trail relative to random locations, but these differences were not significant. Similarly, we observed that late breeding season average bobwhite locations (61.5 m ± 16.5) were closer to the feed trail when compared to random points

Table 3. A compositional analysis simplified ranking of third order habitat and resource selection for northern bobwhite on the supplemental feed treatment area during the early breeding season, Tall Timbers Research Station and Land Conservancy, 2001 – 2007.

YEAR	n	Habitat Rank 5[a]	[b]	Habitat Rank 4		Habitat Rank 3		Habitat Rank 2		Habitat Rank 1
2001	12	unburned upland pine	>	burned upland pine	>	feed trail buffer area	>>>	field	>	drain
2002	39	burned upland pine	>	unburned upland pine	>>>	drain	>	feed trail buffer area	>	field
2003	23	unburned upland pine	>>>	burned upland pine	>>>	feed trail buffer area	>	drain	>>>	field
2005	29	unburned upland pine	>	burned upland pine	>>>	feed trail buffer area	>>>	field	>	drain
2006	44	unburned upland pine	>>>	burned upland pine	>>>	drain	>	drain	>	feed trail buffer area
2007	28	unburned upland pine	>>>	burned upland pine	>>>	drain	>	field	>	feed trail buffer area

[a] An increase in rank value signifies increased use relative to the home range.

[b] The >>> symbol represents significant resource selection preference over lower ranked habitats, and the > symbol represents resource selection preference over lower ranked habitats.

Table 4. A compositional analysis simplified ranking of second order habitat and resource selection for northern bobwhite on the supplemental feed treatment area during the late breeding season, Tall Timbers Research Station and Land Conservancy, 2001 – 2007.

YEAR	n	Habitat Rank 5[a]	[b]	Habitat Rank 4		Habitat Rank 3		Habitat Rank 2		Habitat Rank 1
2001	4	sample size not large enough								
2002	29	feed trail buffer area	>>>	burned upland pine	>	unburned upland pine	>	field	>>>	drain
2003	7	feed trail buffer area	>	unburned upland pine	>	burned upland pine	>	field	>	drain
2005	13	feed trail buffer area	>>>	burned upland pine	>	unburned upland pine	>	field	>	drain
2006	24	feed trail buffer area	>>>	unburned upland pine	>	burned upland pine	>	field	>	drain
2007	19	unburned upland pine	>	feed trail buffer area	>	field	>>>	burned upland pine	>	drain

[a] An increase in rank value signifies increased use relative to the study area.

[b] The >>> symbol represents significant resource selection preference over lower ranked habitats, and the > symbol represents resource selection preference over lower ranked habitats.

(72.3 m ± 18.1), but these differences were not significant (Table 6).

DISCUSSION

Our results demonstrated that on this study area supplemental feeding along a dedicated feed trail reduced the size of bobwhite home ranges during the breeding season. Supplemental feeding has been found to reduce home ranges during the nonbreeding season when feed is spread along roadways or trails (Sisson et al. 2000, Haines et al. 2004) or provided in stationary feeders or localized feeding areas (Frye 1954, Doerr and Silvy 2002, Guthery et al. 2004).

Home ranges sizes on the fed area were consistent from year to year even though a broad spectrum of environmental conditions was observed, including drought conditions in 2007 and above average rainfall in 2003 and 2004 (National Weather Service, Tallahassee Forecast Office). Conversely, home ranges on the control areas were much more variable, especially during 2004 and 2007. Bobwhites select breeding season home ranges that provide suitable protective cover, food resources, nesting, and brooding habitat (Carver 1998). Previous research has documented habitats for nesting and brood-rearing are not limited on Tall Timbers (DeVos and Mueller 1993, Hammond 2001, Palmer et al. 2012). Consistent habitat management between the treatment and control areas suggests larger and more variable home ranges sizes on the control area were likely a function of changing food resources from year to year. During the early breeding season, the burned portion of upland pine habitat had temporarily reduced useable space, which may result in bobwhites moving over larger distances in order to obtain adequate natural food resources, and therefore resulting larger home ranges. However, when a consistent food resource is available, home ranges can remain relatively small and consistent in size, such as what we observed on the supplemental feed treatment area.

For the entire breeding season, bobwhite home ranges on the treatment area included a significant portion of the feed trail. On average, bobwhites had approximately 0.5 km of feed trail available within home ranges. The potentially negative effects of supplemental feeding, such as concentration of predation or disease transference (The Wildlife Society 2006), are often associated with stationary feeding applications (Guthery et al. 2004), where bobwhite activity may be concentrated at a few locations. The potential deleterious effects of concentrated bobwhite locations are less likely when food resources are available along a continuous trail providing all bobwhites access to a relatively large area with available food resources. We believe a long and circuitous feed trail better mimics the scattered patchiness of natural food resources normally available during the breeding season.

Table 5. A compositional analysis simplified ranking of third order habitat and resource selection for northern bobwhite on the supplemental feed treatment area during the late breeding season, Tall Timbers Research Station and Land Conservancy, 2001 – 2007.

YEAR	n	Habitat Rank 5[a]	[b]	Habitat Rank 4		Habitat Rank 3		Habitat Rank 2		Habitat Rank 1
2001	4	sample size not large enough								
2002	29	burned upland pine	>>>	unburned upland pine	>	feed trail buffer area	>	field	>	drain
2003	7	burned upland pine	>	unburned upland pine	>	feed trail buffer area	>	field	>	field
2005	13	burned upland pine	>	unburned upland pine	>>>	feed trail buffer area	>	field	>	drain
2006	24	burned upland pine	>	unburned upland pine	>>>	feed trail buffer area	>	field	>	drain
2007	19	burned upland pine	>	unburned upland pine	>>>	field	>>>	feed trail buffer area	>	drain

[a] An increase in rank value signifies increased use relative to the home range.

[b] The >>> symbol represents significant resource selection preference over lower ranked habitats, and the > symbol represents resource selection preference over lower ranked habitats.

Table 6. Average distance to feed trail for northern bobwhite and random locations on the supplemental feed treatment areas during the early and late breeding season, Tall Timbers Research Station and Land Conservancy, 2001 – 2007.

		Bobwhite Locations		Random Locations	
	n	MEAN	95% CI	MEAN	95% CI
Early Breeding Season					
2002	39	57.3	7.8	66.5	7.6
2003	23	69.8	23.2	72.8	21.1
2005	29	57.6	6.6	73.0	8.2
2006	44	60.7	7.4	68.3	7.7
2007	28	103.6	40.0	110.7	40.1
Late Breeding Season					
2001	4	44.8	7.2	59.3	11.8
2002	30	59.2	12.0	75.7	14.9
2003	8	59.9	9.1	61.7	16.5
2005	13	58.6	10.7	69.5	9.5
2006	25	53.4	11.3	65.6	10.0
2007	19	93.0	48.9	101.8	45.7

Our research supports the conclusion of Buckley et al. (2015) that bobwhites shift home ranges to overlap a reliable food resource. For our study, the second order selection preference for the feed trail buffer area indicates home ranges were orientated to include a higher proportion of feed trail than what was available. Overall, this outcome was consistent for both breeding season time intervals and was observed for all years, regardless of annual and seasonal differences in environmental conditions.

Within home ranges, there was not a consistently high selection preference for the feed trail buffer area relative to the other upland habitats. Miller et al. (this volume) observed that nonbreeding season use of the feed trail buffer area was limited to 14% of the day. While it is possible we did not locate bobwhites frequently enough to document use of the feed trail buffer area, we believe lack of third order selection for the feed trail buffer area supports the idea that bobwhites spent a low percentage of the day using it, similar to Miller et al. (this volume).

Our proximity analysis also supported the conclusion that bobwhites were not significantly adjusting locations closer to the feed trail buffer area. Miller et al. (this volume) similarly found bobwhite coveys during the nonbreeding season were not closer to the feed trail than expected. Presumably, bobwhites were utilizing suitable habitats in the surrounding landscape for other breeding season needs, such as nesting, protective cover, and brood-rearing and only visiting the feed trail buffer area for brief periods as part of their daily habitat use.

A potential conclusion from this experiment is that supplemental food resources resulted in more efficient home ranges, especially during the early breeding season when there are dramatic changes in available habitats due to prescribed fire. Conversely, on the control area the temporary reduction in available habitats from prescribed fire in the early breeding, in addition to the lack of a dedicated food resource, resulted in bobwhites having to move farther distances to meet cover and resource needs and therefore larger and more variable home ranges.

Home ranges for the early breeding season had higher than expected use of unburned upland pine and feed trail buffer area, which were interchangeable as the top 2 ranked resource types. Preference for unburned pine habitat in the early breeding season was consistent with the results of Carver (1998) and supports need for unburned pine habitat in the early season for protective cover and nesting sites. However, preference for burned upland pine in the late breeding season increased when vegetative cover recovered after the spring fires, and also corresponded with increased brood rearing activities. Slight increases in home range sizes during the late breeding season could be attributed to the increased use of burned upland habitats. These outcomes highlight the importance of frequently burned upland pine with similar amounts of unburned upland pine to support bobwhite habitat needs throughout the breeding season for our study area.

MANAGEMENT IMPLICATIONS

Based on this 6 year study, we recommend for managers of properties of similar habitat conditions and management goals to utilize broadcast supplemental feeding along a continuous feed trail, during the breeding season. This is especially important during the early breeding season when habitat management and prescribed burning may reduce useable space and cause bobwhites to move larger distances to meet resource needs. For pine savanna habitats, we recommend prescribed burning to produce a mix of burned and unburned patches along with supplemental feeding to increase habitat suitability and reduce movements and home range size of bobwhites.

ACKNOWLEDGEMENTS

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DO MOVEMENT PATTERNS AND HABITAT USE DIFFER BETWEEN OPTIMAL- AND SUBOPTIMAL-SIZED NORTHERN BOBWHITE COVEYS?

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ABSTRACT

The group size of social animals and spatial structure of the environment can affect group behavior and movement decisions. Our objective was to investigate movement patterns and habitat use of northern bobwhite coveys (*Colinus virginianus*) of different size. Using radiotelemetry, we continuously monitored covey group size, daily movement, and habitat use on 12 independent 259-ha study areas in eastern Kansas, USA, during the winters between 1997 and 2000. We used correlated random walk models and fractal dimension models to determine if covey size affected movement characteristics or habitat selection. Intermediate-sized coveys (9–12 individuals, close to optimal covey size) exhibited daily movements that were substantially smaller and weekly home ranges that were more composed of woody escape cover than coveys of smaller or larger sizes. From the fractal dimension analyses, these coveys exhibited movement in between linear and a random walk at small spatial scales but very linear at large spatial scales. Large coveys had increased daily movement and tended to move in straighter lines (as indicated by the high proportion of turning angles [i.e., the angle between an initial direction and a new direction] around 0° and 180° and their multiscale fractal dimension) and they incorporated more cropland into their range, presumably to meet the feeding requirements of a larger group. In contrast, small coveys (1–4 individuals) tended to move more and increase the size of their home range, travel with a greater diversity of turning angles, and show movement patterns that were largely tortuous across a greater number of habitat patches at larger spatial scales (700 m). Small coveys have lower fitness and add new membership to increase fitness so it is possible that the movement behavior we observed represented a shift into a foray mode where bobwhites were searching for new membership. For areas with small populations and covey sizes, this information will help biologists better plan for habitat management to assist these coveys with their winter fitness.

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Key words: *Colinus virginianus,* correlated random walk, fractal dimension, habitat fragmentation, northern bobwhite, optimal group size

Population processes partially depend upon the spatial structure of the environment in which individuals occur (Turner and Gardner 1991, Tilman and Kareiva 1997, Turchin 1998) and individual behavior and movement decisions within a heterogeneous space can affect fitness (Okubo 1980, Kareiva 1990, Bell 1991, Levin 1992, Zollner and Lima 1999). Therefore, investigating the interplay between movement behavior and spatial structure provides a mechanistic link between ecological processes and the spatial landscape mosaic (Nathan 2008, Nathan et al. 2008). This relationship between behavioral ecology and landscape ecology is not only of growing ecological interest (Lima and Zollner 1996) but is of fundamental importance to understanding the population dynamics of mobile species (Merriam et al. 1991, Johnson et al. 1992).

To better understand the role of spatial structure in individual movement decisions, there has been increasing development and testing of individually based models (DeAngelis and Gross 1992, Judson 1994) in which movement is often the central component (Real et al. 1992; Johnson et al. 1992; Turner et al. 1993, 1994; Tischendorf 1997). Using individually based models has the advantage of taking into account the state of the animal and how that state changes according to the animal's actions and the environment. This can provide a greater degree of biological realism in assessing the relationship between an animal's behavior and surroundings (Houston et al. 1988).

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Several types of simple individually based models have been used successfully to test how individual behavior influences movement. First, correlated random walk (CRW) models summarize complex data on movement patterns, reducing movement paths into measures of movement distances over short time intervals and turning angles (e.g., daily). Correlated random walk models have been used to understand the search strategies behind specific behaviors (Kareiva and Shigesada 1983, Bovet and Benhamou 1988, Marsh and Jones 1988, McCulloch and Cain 1989, Olson et al. 2000). Turchin (1996) has recommended CRW models as the null hypothesis when analyzing paths of animal movement. Second, analyses of fractal dimension have been used to relate paths of animal movement to the spatial patterns of resource distribution (Crist et al. 1992; With 1994*a,b*; Etzenhouser et al. 1998; With et al. 1999; Marell et al. 2002). Rarely, however, have these 2 methods been used in conjunction to analyze animal behavior within the landscape (Crist et al. 1992, Marell et al. 2002).

To date, empirical studies that test individually based models of organismal movement patterns have primarily focused on the foraging patterns of insects (Kareiva and Shigesada 1983, Turchin 1991, Crist et al. 1992, With 1994*a*). Although research has investigated long-term movements of vertebrates (Benhamou 1990, Ward and Saltz 1994, Focardi et al. 1996), especially across large spatial scales (Koenig et al. 1996, Bergman et al. 2000, Cushman et al. 2005, Dai et al. 2007, Forester et al. 2007, Fryxell et al. 2008), there has been little work to consider how social rank within groups (e.g., Wittemyer et al. 2008) or how dynamics and/or maintenance of optimal and suboptimal group size affects movement decisions. Northern bobwhite (*Colinus virginianus;* hereafter, bobwhite), is a nonmigratory bird species that often uses edge habitat and treeline corridors to travel and forms social groups of 2–22 individuals, called coveys, during the nonbreeding season (approx. Sep–Apr; Brennan 1999). Northern bobwhite maintain an average covey size of 11 individuals and, as covey size becomes smaller or larger, behaviors (e.g., distance moved, alert vs. feeding behavior) will change and survival will decline (Williams et al. 2003). Bobwhites experience high rates of winter mortality (Pollock et al. 1989, Burger et al. 1995) so covey size reduction occurs readily. Individuals in small coveys focus their behavior on finding new membership (often joining another small or intermediate-sized covey) to increase fitness (Bartholomew 1967, Yoho and Dimmick 1972, Williams et al. 2003). In contrast, individuals in large coveys show reduced feeding efficiency and necessarily spend more time foraging. However, it is not known whether group size can influence individual movement patterns via rapid linear paths to a required resource (e.g., food or new membership) or through longer explorations where animals drift into new territory or use forays into neighboring unknown areas followed by a return to their home range (Koenig et al. 2000, Conradt et al. 2003).

Spatio-temporal analyses of movement patterns in mobile species provide an approach for studying search-strategy behaviors associated with foraging, predator avoidance, or group size maintenance (Benhamou 1990). Additionally, extrapolating individual decisions to the landscape scale is of interest to behavioral and landscape ecologists (Lima and Zollner 1996) and is critical to understanding population processes. The specific objective of our study was to use random walk and fractal dimension models to quantify how movement patterns differ between small or large (suboptimal) and intermediate (optimal) covey sizes and how these patterns may be influenced by habitat structure at different spatial scales.

STUDY AREAS

We conducted our research on 12 259-ha parcels of private and public land in eastern Lyon, western Osage, and western Coffey counties, Kansas, USA. Each study area was separated by a minimum of 1.6 km (range = 1.6–18.4 km). Winter bobwhite covey ranges are between 4 and 20 ha (Roseberry 1964, Bartholomew 1967, Yoho and Dimmick 1972, Williams 1996); therefore, we assumed distances between study areas were large enough to prohibit interchange of bobwhites among study areas.

Habitat types on study areas comprised on average 35% cropland (e.g., grain sorghum [*Sorghum bicolor*], soybean [*Glycine max*], wheat [*Triticum* spp.]), 27% native tallgrass rangeland (e.g., big bluestem [*Andropogon gerardii*], little bluestem [*Schizachyrium scoparium*], indiangrass [*Sorghastrum nutans*], switchgrass [*Panicum virgatum*]), 11% native grass under Conservation Reserve Program guidelines, 12% idleland (e.g., treelines, hedgerows, farmsteads, and old fields), 6% woodland, 5% water or marshland, and 4% hayland. All study areas consisted of habitat that was representative of east-central Kansas (Byram 1996) and no recreational hunting occurred.

METHODS

We captured bobwhites between 1 October and 31 January from 1997 to 2000 using bait-traps (Stoddard 1931) and nightlighting (Labisky 1968). Upon capture, we determined sex and age of birds (Rosene 1969), and weighed them to the nearest gram. From each covey we randomly selected (i.e., regardless of sex or age of other birds radioed in the covey) $\geq$3 birds weighing $\geq$150 g and fitted each with a necklace-type radiotransmitter weighing $<$6 g (Burger et al. 1995). We did not radiomark birds weighing $<$150 g to prevent stress from radiocollars (i.e., radiocollars $<$5% of body mass; Samuel and Fuller 1994). We leg-banded all other captured birds in the covey. We immediately released all birds at the capture location. We located radiotagged individuals approximately 5 times/week by homing (White and Garrott 1990) between 9 November until death, radio failure, or 31 January 1997–2000. We systematically varied location times over all diurnal hours to capture a full range of behavioral variation. We recorded individual locations as Universal Transverse Mercator coordinates (Exum et al. 1982). We attempted to estimate size of the covey containing radiocollared individuals every week between 9 November and 31 January via flush counts. Reliance on flush counts to estimate covey size can be biased (Janvrin et al. 1991); therefore, we created a "diary" of covey membership and size over time by supplementing weekly flush counts with information gathered from continuous trapping of banded and radiocollared birds as well as from known live and dead birds identified via radiolocations. Anecdotally, these complimentary data sets tended to provide a consistent and predictable estimate of covey membership.

To determine whether covey size influenced covey movement patterns, we examined only coveys that had both 1) an estimated covey size for the week (covey only flushed once per week) and 2) 5 consecutive radiolocations within a week. If a covey was radiolocated <5 times or the covey size was unknown during the same time interval, we removed the covey from analysis. To avoid pseudoreplication, if a covey size remained the same over multiple weeks, we only included the first week of data. Each covey-week was considered as an independent sampling unit and would contain 5 locations, 4 daily path distances, 3 turning angles, and an estimated covey size. We measured effect of covey size on distance the covey moved per day using linear regression ($\alpha \leq 0.05$) and Mallow's C_p statistic (Draper and Smith 1981) to find the best-fit trend.

Correlated Random Walk Models

To test statistically whether animal movement is nonrandom, a CRW model should be considered as a null hypothesis. Correlated random walk models assume independent distributions of move lengths and turning angles that describe an animal's movement path. Although each move consists of random draws from each of these 2 distributions, the moves are considered correlated because the turning angles are not distributed uniformly around a circle but rather movement occurs in a preferred direction around which there is random variation. Correlated random walk models assume there are no long-term movement strategies—specifically, that movement in one day depends only on movement in the preceding day. The expected displacement of coveys over time is given by

$$R_n^2 = n \times (l_1) + 2 \times (l_2^2) \times \left(\frac{c}{1-c}\right) \times \left(n - \frac{1-c^n}{1-c}\right) \quad \text{(Eq. 1)}$$

where R_n^2 is the net squared displacement from the first location (m^2), n is the number of subsequent moves from the first location, l_1 is the mean squared move distance (m^2), l_2 is the mean move distance (m), and c is the mean of the cosines of the turning angles (Bovet and Benhamou 1988). Observed movement can be tested against the null model of the CRW model to identify long-term strategies. For example, if the turning angle in one day is negatively correlated with the turning angle in the preceding day (in violation of the assumption of the CRW model), coveys will tend to move in a straight line and movement displacement after several days will be greater than that predicted under the null CRW model. If the log-predicted displacement divided by observed displacement were equal to zero (one-sample t-tests, $P \leq 0.05$), we would conclude that the covey moved in a correlated random walk. If the model overpredicted displacement, then the tested covey size would show preference for a region. Lastly, if the model underpredicted displacement, then the tested covey size would show greater directional movement that could be inferred as avoidance of a region (Bergman et al. 2000). First we tested for uniformity of turning angles by a Rayleigh's test of Uniformity ($P \leq 0.01$) and Chi-square analysis of turning angles distributions using Program ORIANA 3.13 (Rockware, Inc., Golden, CO, USA). Second, we examined a correlated random walk model as a descriptor of movement of small, intermediate, and large-sized coveys. For these tests, we combined data from pathways recorded for different coveys within the same size categories; preliminary analyses found no consistent differences among covey-weeks.

Fractal Dimension Analysis

We examined the fractal dimension of movement patterns shown by small (<9 individuals), medium (9–12 individuals), and large (>12 individuals) coveys. Fractal dimension analysis of animal movement provides a method for assessing species' behavioral responses to landscape heterogeneity at multiple scales (Milne 1991, With 1994*b*). The fractal dimension D indexes overall tortuosity (complexity) of an animal's movement pattern. Tortuosity of animal paths represents their reaction to landscape heterogeneity in which they translate environmental stimuli into movements (Dicke and Burrough 1988, Crist et al. 1992, With 1994*b*). Theoretically, in two-dimensional space, tortuosity can range from 1—indicating a straight line—to 2—indicating a Brownian diffusion or random walk that essentially fills a plane. Linear movement patterns (D = 1) typically indicate directed movements that offer little resistance and where the landscape is viewed as homogeneous by the organism, while D = 2 indicates convoluted movement patterns typical of animals using a structurally complex environment (Wiens and Milne 1989; Crist et al. 1992; With 1994*a*, *b*). We calculated fractal dimensions for average weekly movement of coveys across multiple spatial scales using the VFRACTAL program implemented with the modified dividers method to account for truncation error (Nams 1996, Nams 2006).

Habitat Use

To determine whether covey size affected habitat selection differently, we compared average study-area habitat availability to average habitat used per covey-week. We digitized land cover in the 12 study areas from aerial photographs using ArcView and we ground-truthed all land-use maps to assure accuracy. We divided major land-use categories across all study areas into pasture (23.3 ± 6.0% SE), hayland (2.6 ± 1.3% SE), cropland (33.0 ± 6.3% SE), idle grassland (including roadsides,

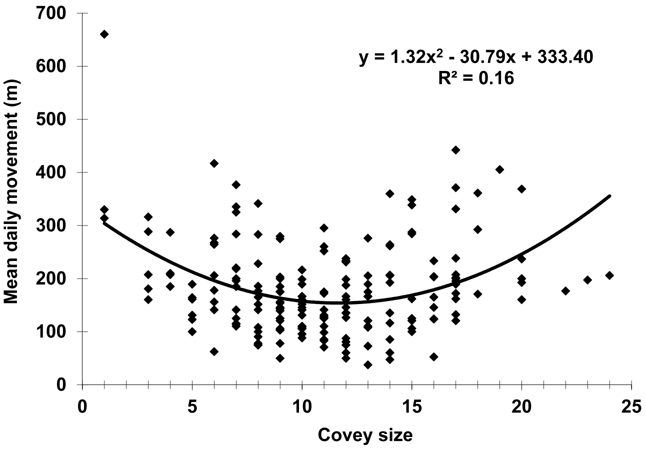

Fig. 1. The effect of covey size on mean daily movement (m) of northern bobwhite coveys in East-central Kansas, USA, 1997–2000. Solid line indicates quadratic relationship ($F_{2,192} = 17.79$, $P < 0.01$) estimated by regression.

Conservation Reserve Program and native grassland, grassy waterways, and old fields: 22.8 ± 5.9% SE), and woody vegetation (mainly corridors, 33.0 ± 6.3% SE). We considered a covey's habitat use as the average percentage of cover types observed within the independent covey-week. We used multivariate analysis of variance with Tukey's *post hoc* test with Bonferroni adjustments ($P \leq 0.05$) to determine overall variability in habitat use among different covey sizes and with average study area habitat availability.

RESULTS

Across all 3 years, 195 covey-weeks were available for analysis (i.e., were followed for 5 consecutive days within a week, the covey size was estimated, and any subsequent covey-weeks with the same covey size were excluded to avoid pseudoreplication). Covey size was related to mean daily movement in a convex manner ($F_{2,192} = 17.79$, $P < 0.01$), where both small and large coveys traveled greater distances than intermediate-sized coveys (Fig. 1). For further analysis, covey sizes were combined into categorical groups 1–4, 5–8, 9–12, 13–16, and ≥17 individuals (Table 1).

All covey size categories, except the smallest group (Rayleigh's test for uniformity $P = 0.11$), exhibited a nonuniform distribution of turning angles (Rayleigh's test for uniformity, $P < 0.01$) with prevalence toward turning angles of approximately 180°, especially for small and large coveys (Table 1). Coveys of intermediate size also tended to have a greater proportion of turning angles at 0° (Fig. 2). Additionally, small coveys (1–4 and 5–8) showed a broader distribution of turning angles (Fig. 2) than medium and large coveys (9–12, 13–16, ≥17 individuals; Chi-square analysis; Table 2). Using the correlated random walk model, we found weekly displacement showed preference for a region ($t > -4.40$, $P < 0.01$), with statistically indistinguishable differences among covey size categories ($F_{4,190} = 1.98$, $P = 0.10$; Fig. 3). Additionally, examining the autocorrelation of successive turning angles for different covey sizes showed consistent negative first-order and second-order correlations for all covey sizes. For example, if a covey moved in the same direction for 2 successive days, then it was less likely to continue moving in the same direction in the third day. This made the weekly displacement of coveys less than predicted by the CRW model.

Analyzing the fractal dimension of movement patterns, we found that the movement of small coveys (1–4 individuals) increased toward 2—the fractal dimension of a random walk—with increased scale. This observation indicates that the searching behavior of small coveys was more directed at small scales (100 m: D = 1.34) but became more tortuous at larger scales (700 m: D = 2.00). Because habitat patches are typically several hundred meters in diameter, this result suggests that movement of small coveys within habitat types (small scales) is directed, whereas movement among types (large

Table 2. Chi-square value (df = 17) of turning angles of different categories of northern bobwhite covey size in East-central Kansas, USA, 1997–2000. Analyses test the probability associated with the null hypothesis that samples are drawn from the same population.

Covey size	1–4	5–8	9–12	13–16	≥17
1–4	—				
5–8	18.24	—			
9–12	32.89**	24.20	—		
13–16	28.99*	34.26**	11.92	—	
≥17	24.49	24.17	23.98	26.71	—

* $P < 0.05$.
** $P < 0.01$.

Table 1. Descriptive statistics of daily path distances and turning angles of northern bobwhite covey sizes in East-central Kansas, USA, 1997–2000.

Covey size	Sample size: Covey-weeks	Sample size: Daily path distances	Sample size: Turning angles	Mean daily move distance (m) (SE)	Mean angle of successive move (°) (SE)	Angular concentration[a]	Rayleigh's test of uniformity, P
1–4	12	48	36	278.9 (38.8)	182.7 (15.6)	0.54	0.11
5–8	44	176	132	183.2 (13.2)	239.0 (15.2)	0.47	<0.01
9–12	74	296	222	147.0 (6. 5)	168.3 (45.4)	0.12	<0.01
13–16	40	160	120	172.4 (13.2)	127.7 (27.3)	0.27	<0.01
≥17	25	100	75	237.3 (18.0)	185.7 (9.2)	1.08	<0.01

[a] The angular concentration is a parameter that measures the departure of the distribution from a perfect circle (or a uniform distribution).

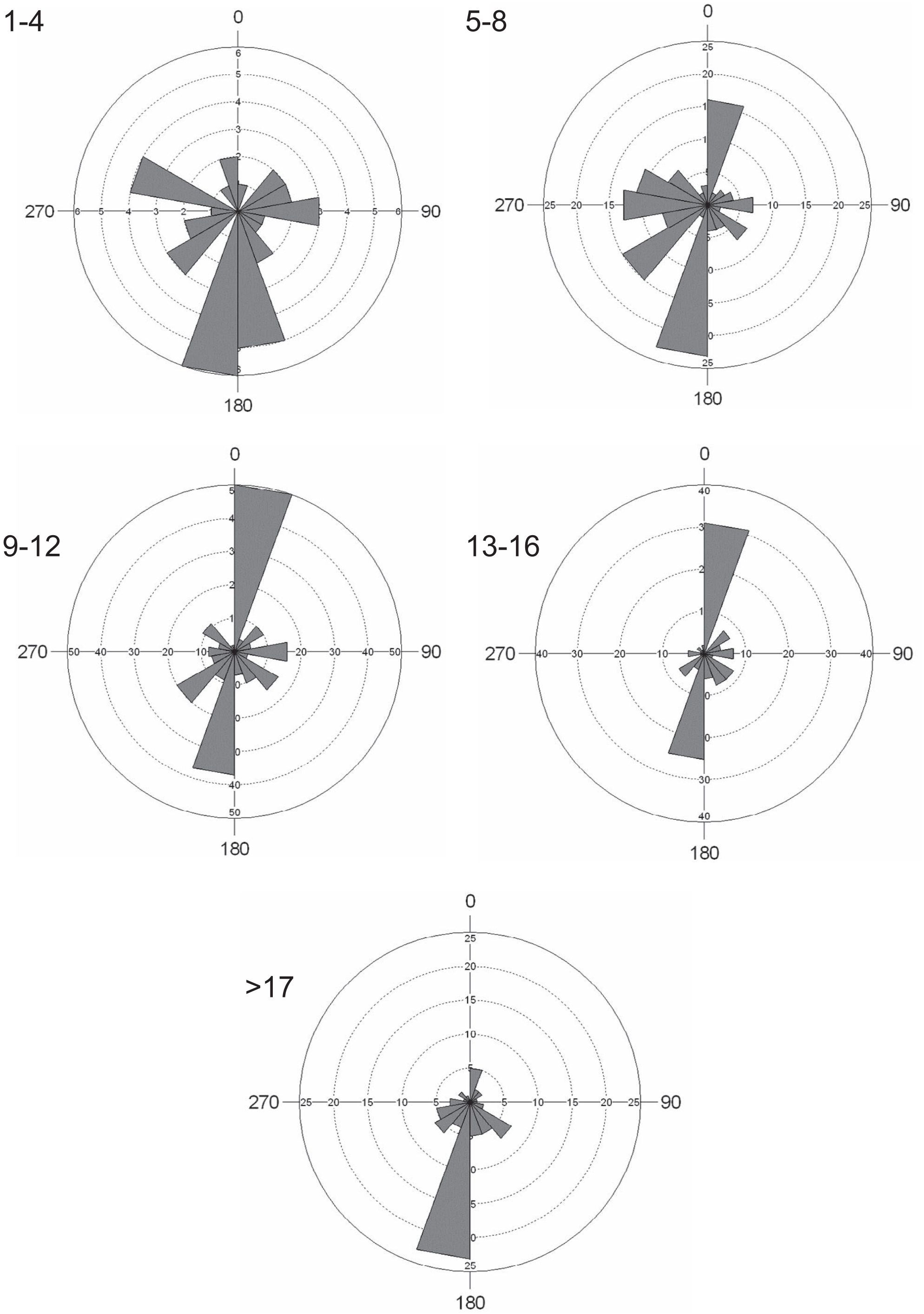

Fig. 2. Angular distributions of successive turning angles for northern bobwhite covey sizes in East-central Kansas, USA, 1997–2000. The length of the bars indicate the number of data points that fit the specific angular concentration.

scales) is more complex. Intermediate (9–12 individuals) and moderately large coveys (13–16) show the opposite search behavior. Although their small-scale (100 m) movement patterns are moderately directed (D = 1.56–1.62), at larger scales their movement patterns become strongly linear (D = 1.00 for both; Fig. 4). This suggests that coveys of intermediate size (9–16 individuals) make a thorough search of habitats (perhaps for food resources) at smaller scales. Yet at larger scales they tend to move linearly among habitat types (such as through linear corridors of woody cover). The largest coveys (≥17 individuals), who tended to have increased daily movement, showed an interesting oscillation in fractal dimension, producing an average D = 1.37.

Pasture was used in relatively equal percentage to its availability and across coveys of all sizes, although small coveys (1–4 individuals) tended to use it slightly less than coveys of all other sizes (Fig. 5). Hayland was also used

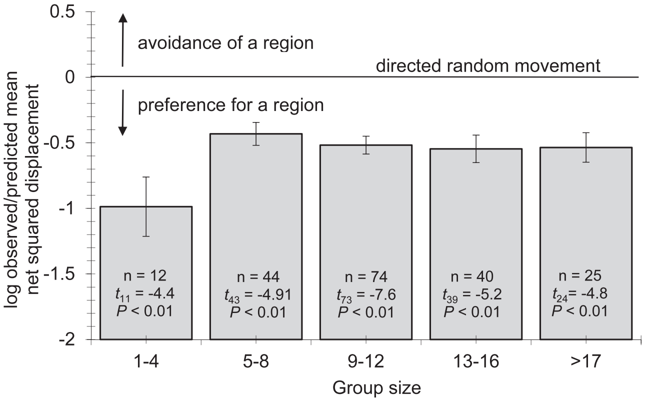

Fig. 3. Observed/predicted weekly displacement (R^2, eq. 1) of northern bobwhite coveys from a correlated random walk model (±2 SE) in East-central Kansas, USA, 1997–2000. Values >0 indicate observed weekly displacement was more directive than estimated from a correlated random walk (CRW), values $=0$ indicate correspondence to a CRW, and values <0 indicate fidelity for an area. One sample *t*-test ($P < 0.05$) measures significant departure from CRW.

in relatively equal percentage to its availability and across coveys of all other sizes. Idleland (such as Conservation Reserve Program grasslands and grassy waterways) was used differently across coveys and small coveys (1–4 individuals) used idleland more than average (9–12 individuals) and large ($>$17 individuals) coveys. Woody cover (primarily linear corridors of treelines and woodlots) was used differently across groups and average-sized coveys (9–12 individuals) used woodland more than large ($>$17 individuals) coveys. Woody cover (often associated with edge habitat) is generally preferred by northern bobwhite for daytime escape cover; therefore, this result seems to indicate coveys of intermediate size have ranges that allow them to take advantage of higher quality habitat. Last, cropland was used differently across groups and coveys of 5–8 individuals used it less than the largest coveys ($\geq$17 individuals).

DISCUSSION

In the growing effort to establish a movement ecology paradigm, it is critical that ecologists not only understand the interplay between movement behavior and spatial structure (Nathan 2008, Nathan et al. 2008) but also how social structuring of animals could add complexity to this paradigm (Wittemyer et al. 2008). Williams et al. (2003) demonstrated in the same area that northern bobwhite coveys of roughly 11 individuals were optimal, corresponding to the greatest fitness achieved by their members. Small coveys (1–7 individuals) had lower group persistence and individual survival and used increased movement to create or join larger coveys where survival was higher, while large coveys (15–22 individuals) had lower individual survival, increased group movement, and individual mass loss (Williams et al. 2003). Density-dependent feedbacks (e.g., lower survival and increased competition) may have reduced larger coveys to a stable size. Williams et al. (2003) results suggested the regulation of an optimal group was promoted by high group persistence, low group movement, improved feeding efficiency, improved individual predator detection, and improved individual survival. On account of these complex optimal group size dynamics, we hypothesized that coveys could have the potential to respond to their environment in different ways depending on their size and deviance from optimal covey size.

Movement patterns of different-sized coveys depended on the scale at which they were measured. With (1994a) suggested departure from random search patterns reflects encounters with the physical structure of the vegetation or responses to correlates of patch structure. Consequently, routine daily movements within a covey's home range will largely dictate bobwhite habitat use and landscape perception. This movement was based on remembered characteristics of the landscape, forage quantity and quality, and escape cover quantity and quality. Indeed, increased knowledge of the landscape around these coveys probably allowed them the ability to make strategic 'decisions' regarding their movements and needs (Lima and Zollner 1996, Marell et al. 2002). We initially questioned whether covey size could affect movement rates and patterns via either directed-and-quick movements or through longer forays where animals drift into new territory and/or then return to the initial home range. From our coarse daily analysis, the way different covey sizes departed from random movement indicated that different behavioral states (associated with covey size) could influence perception and use of the landscape. We encourage future researchers to replicate our efforts using the recent technological advancements of Global Positioning System radiocollars with data loggers with very short temporal resolutions because this should strengthen our understanding of these movement processes.

In this study, coveys of intermediate size (9–12 individuals, close to optimal group size) exhibited daily movements that were substantially smaller and weekly home ranges that consisted of more woody escape cover than was exhibited by coveys of smaller or larger sizes. From the fractal dimension analyses, these coveys exhibited movement in between linear and a random walk at small spatial scales but very linear at large spatial scales. Thus, at larger spatial scales, habitat use became largely homogeneous as would be expected by increased selection for woody cover. Woody cover generally acts as escape cover and a mode for travel (Williams et al. 2000); therefore, increased linear movement within these corridors by coveys of intermediate size would enhance their observed increased fitness (Williams et al. 2003).

However, the relationships observed by large and small coveys showed a different result. Large coveys ($\geq$17 individuals) are known to have lower feeding efficiency and fitness (Williams et al. 2003) yet low probabilities of breaking apart into smaller coveys. Williams et al. (2003) hypothesized behavioral patterns of large coveys reflected more concern with feeding than with adjusting membership to create a more intermediate-sized group. In the present study, large coveys had increased daily movement relative to smaller coveys and

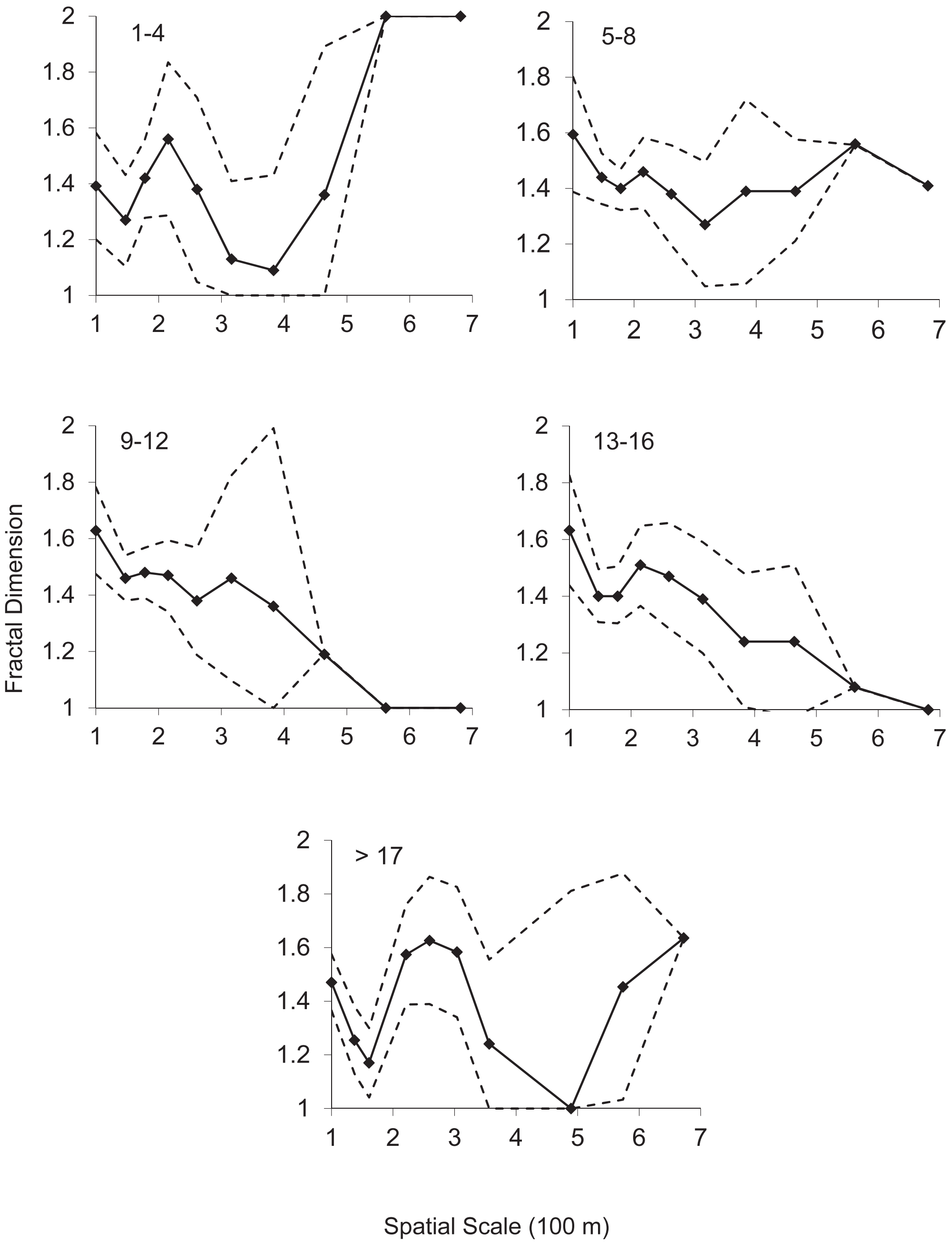

Fig. 4. Fractal dimensions D (±95% CI indicated by dashed lines) across scales for different covey sizes of northern bobwhite coveys in East-central Kansas, USA, 1997–2000.

tended to move in straighter lines (as indicated by the high proportion of turning angles around 0° and 180°, and their multiscale fractal dimension) and they incorporated more cropland into their range, presumably to meet the feeding requirements of a larger covey. These results support the idea that large coveys are using complex searching behavior within larger home ranges containing more complex habitat structure as a response to increased nutritional demands.

In contrast, small coveys (1–4 individuals) tended to move more and increase the size of their home range, travel with a greater diversity of turning angles, and show movement patterns that were largely tortuous across a greater number of habitat patches at larger spatial scales (700 m). Small coveys have lower fitness and add new membership to increase fitness (Williams et al. 2003) so it is possible that the movement behavior we observed represented a shift into a foray mode where they were searching for new membership (Conradt et al. 2003) by making themselves known through morning epideictic displays (Stokes 1967). Indeed, the difference in movement patterns in small coveys (that are searching for new membership) as compared with movement patterns of large coveys (that are presumably dominated by feeding) supports Fletcher's (2006) argument that incorporating

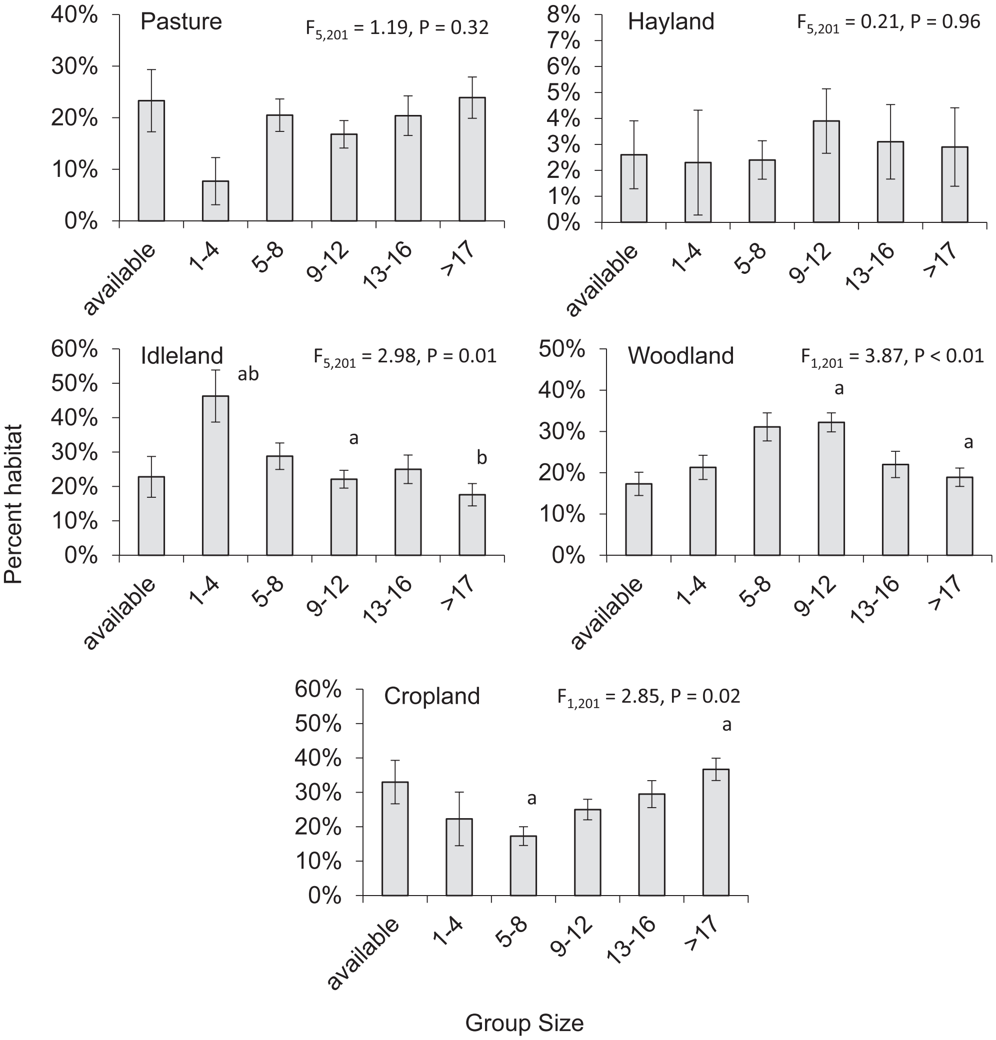

Fig. 5. Average percent habitat availability across all 12 study areas and average percent habitat use (±SE) by different covey sizes of northern bobwhite in East-central Kansas, USA, 1997–2000. Multivariate analysis of variance ($P < 0.05$) was tested for differences among groups. Like letters indicate differences between pairs of groups using Bonferroni adjusted Tukey's *post hoc* test ($P < 0.05$).

conspecific attraction into movement decisions greatly alters habitat selection and population dynamics.

Use of corridors to aid animal movement from one habitat patch to another for improving resource acquisition has generated substantial recent interest (e.g., Henein and Merriam 1990, Saunders and Hobbs 1991, Rosenberg et al. 1997, Gilliam and Fraser 2001, Mabry and Barrett 2002, Berggren et al. 2002). Within this context, Lima and Zollner (1996) argued that an important unanswered behavioral question is whether corridors are perceived (i.e., sought out) as travel routes to other patches or whether they are simply landscape elements into which animals passively enter. During the nonbreeding season, northern bobwhites use a variety of habitat types but nonetheless rely heavily on edge corridors (treelines, hedgerows, etc.), not only for escape cover but also for daytime travel between grassland and agricultural fields for feeding and roosting (Williams et al. 2000). In this study, we found this to be especially true for coveys of intermediate size. Immigration and emigration are critical to group-size maintenance via covey fission and fusion; therefore, distribution and spatial arrangement of woody corridors might influence the maintenance of optimal covey size. This type of relationship has been seen in Florida scrub jay (*Aphelocoma coerulescens*) groups where habitat fragmentation can inhibit movement between groups and disrupt the maintenance of a stable group size (Stith et al. 1996). However, in the case of small coveys, corridors may not be as crucial a mechanism to finding new membership. Small coveys appear to travel with a greater diversity of turning angles and have movement paths with high tortuosity at larger spatial scales; therefore, they appear willing to move outside of habitat corridors as a means of travel from one patch to another when maintenance of group size is important. Fletcher (2006) further hypothesized that conspecific attraction (e.g., the epideictic displays produced by bobwhite; Stokes 1967) would become increasingly important in fragmented landscapes where travel corridors may not always exist. Although we found linear woody corridors were important for covey size maintenance, small coveys appeared to move via forays across other types of fragmented habitat supporting Conradt et al.'s (2003) and Fletcher's (2006) hypotheses.

Northern bobwhites are primarily short-distance ground-travelers that make occasional short flights (we observed average daily movement = 183 m and the farthest 1-day distance = 1,100 m); therefore, we suspect they have relatively limited perceptual ranges. Consequently, any barrier approximately >1 km in width is unlikely to be crossed despite the presence of conspecific attraction. Management plans designed to enhance northern bobwhite populations should include recommendations for developing corridors or patches juxtaposed between useable habitat to avoid long-distance barriers. Our results also suggest that if population expansion is of priority, there is a need to examine further whether habitat management should be focused on expansion of the number of optimum covey ranges (with smaller, less complex areas) or on promoting ideal conditions for large coveys (with larger, more complex areas).

MANAGEMENT IMPLICATIONS

Comparisons of northern bobwhite movement patterns suggest that bobwhites respond to their environment differently depending on covey size. Additionally, covey movements may have the potential to affect habitat use, foraging success, and group fission and fusion dynamics. All of these factors have the potential to affect overwinter survival, which is critical for increasing bobwhite numbers (Sandercock et al. 2008). Of particular importance, in portions of the bobwhite range where populations are small with the possibility of smaller and isolated coveys, managers should be aware that bobwhites potentially will take larger forays across habitat types, thus increasing the likelihood of daily mortality risk. Thus we believe it is important that habitat management goals include the development of as many corridors with escape cover as possible to decrease predation risk or to enhance contiguity of habitat components, such as development of old field habitats where all components are in close juxtaposition.

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FORAGING BEHAVIOR OF NORTHERN BOBWHITES IN RELATION TO RESOURCE AVAILABILITY

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ABSTRACT

Distribution of food resources may influence northern bobwhite (*Colinus virginianus*) foraging decisions and demographic rates. We tested whether covey movements were sensitive to food availability by spreading sorghum (*Sorghum bicolor*) every 15 days at 3 rates; high rate (174 L/ha/yr), low rate (44 L/ha/yr), and no feed on 3 sections (~240 ha each) of Tall Timbers Research Station, 2009–2010. We measured sorghum availability spread along a 17 km feeding trail every 5 days. We determined seasonal (1 Nov - 15 Mar) home ranges of radio-tagged coveys ($n = 89$) and daily movement rates and home ranges of a subset of coveys located every 30 mins, sunrise to sunset (1 Feb - 15 Mar). Diet was determined from harvested bobwhites. Mean sorghum availability (seeds/0.5m^2) on the feed trail declined from 50 seeds at day 1 to 12 seeds at day 15, and 11 seeds at day 1 to 0 seeds at day 10, for high and low rates, respectively. Seasonal home ranges did not differ among treatments; however, daily home ranges were smaller for coveys on the high rate areas, as was dispersion of locations within home ranges. Distances to the feed trail from covey and random locations were similar. There was no difference in distance traveled (25.20 m; SE = 0.65) between consecutive covey locations among treatments. Proportion of sorghum in the diet declined precipitously when <15 seeds/0.5m^2. We estimated an empirical giving up density of 10–14 seeds/0.5m^2, ~1.6 kcals/0.5m^2. Food availability, even at high levels, marginally affected covey space use and movement rates during late winter. Other factors affecting bobwhites, such as predator avoidance, or thermal regulation, may have a more significant effect on bobwhite covey daily movements and space use.

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Key words: behavior, foraging movements, northern bobwhite, range, supplemental feed, telemetry

INTRODUCTION

Providing supplemental food resources, through habitat manipulation, establishment of food plots, or direct distribution of wildlife feed has been a common practice in wildlife management (The Wildlife Society, 2006) and bobwhite management specifically (Stoddard 1931, Rosene 1969, Robel et al. 1974, Landers and Mueller, 1986, Guthery et al. 2004). More recently, bobwhite managers spread cereal grains, typically corn (*Zea mays*) or sorghum, along dedicated feed trails through bobwhite habitat (Michener et al. 2000, Sisson et al. 2000, Haines et al. 2004, Whitelaw et al. 2009, Wellendorf et al. this volume). Supplemental feed trails are relatively long, averaging 2.4 km of feed trail per 40.5 ha of bobwhite habitat based on a survey of 12 managed properties in the Red Hills (Wellendorf et al. this volume). Typically, supplemental feed is distributed into bobwhite habitat from a tractor mounted spreader across a 10–20 m band on the feed trail every two weeks such that approximately 62–125 kg of grain are spread per hectare (e.g., 1–2 bushels/acre) of habitat on an annual basis. Herein, we define supplemental feeding as spreading cereal grains along a dedicated feed trail through bobwhite habitat as detailed in Wellendorf et al. (this volume) and the "feed patch" as the area over which grain is spread.

Bobwhites readily use cereal grains even when habitat provides abundant and diverse natural food resources. Whitelaw et al. (2009) reported that sorghum accounted for over 67% of bobwhite diets on 2 intensively-managed areas that spread supplemental feed. Bobwhite managers spread cereal grains in part to

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improve hunting and believe spreading supplemental feed localizes coveys increasing their accessibility to the area around the feed patch searched by pointing bird dogs. If true that coveys reduce their daily home range and localize movements near the feed patch, hunting within or near the feed patch should improve hunting success and increase harvest. However, if false, hunters focusing effort in or near the feed patch may experience reduced hunting success except when bobwhite are using the feed patch.

In general, increased susceptibility to harvest from providing supplemental feed to game species is a concern of professional biologists (The Wildlife Society, 2006). DeMaso et al. (1999) found that using feeders to provide grain to bobwhites increased the proportion of bobwhite mortality attributed to harvest, but did not increase overall mortality rates of bobwhites. Townsend et al. (1999) and Sisson et al. (2000) found supplemental feeding did not increase harvest rate of bobwhites or predispose bobwhites to predation. Limited research on bobwhite movements in relation to supplemental feeding found smaller home ranges on fed sites, suggesting bobwhites may shift space use to the areas with supplemental feed (Sisson et al. 2000, Buckley et al. 2015). Sisson et al. suggested that bobwhites in the supplemental fed area had lower susceptibility to harvest because they spent less time feeding and more time displaying escape behaviors than bobwhites without access to supplemental feed.

Optimal Foraging Theory (OFT) predicts that foragers ignore low "profitability" food items when more profitable food items are abundant and available (Stephens et al. 2007). Sorghum spread along the feed trail provides an abundant and recurring source of high energy (i.e., profitable) food for bobwhites. As highlighted previously, bobwhites include supplemental feed as a major diet item (Whitelaw et al. 2009), therefore they obviously use the feed patch. However, it is unknown how much time bobwhites associate with the feed patch, how it affects their overall space use, or how many seeds of grain per unit area is required to elicit changes to their behaviors. Therefore, we determined bobwhite use of the feed patch and how bobwhites moved in relation to the feed patch to better understand the likelihood that supplemental feeding localizes bobwhites movements and potentially increases their susceptibility to hunters.

The currency by which bobwhite choose to remain or leave a patch is energy gained per unit of time spent foraging (Stephens et al. 2007). The marginal value theorem (Charnov 1974) of OFT predicts bobwhites within the supplemental feed patch experience diminishing foraging returns as grain seeds decline in abundance over time requiring increasing effort per seed. At some unknown availability of seeds remaining in the feed patch, a foraging threshold is reached and the currency of the feed patch will decline to or below the currency available in natural feed patches. At this foraging threshold bobwhites should reduce use of the feed patch, or abandon the patch, and choose to forage in patches with more profitable natural sources of food. In this context, we assessed how bobwhites used the supplemental feed patch by determining their diet and use of the patch in relation to availability of sorghum seeds per unit area. We measured when bobwhites shifted their use from the feed patch and foraged more on other food items as an empirical "giving up density" of grain, or the energy per unit area at which foraging within the feed patch was no longer profitable (Brown et al. 1988).

The mechanisms through which food availability influences demographic parameters are poorly understood. While several studies demonstrated equivocal effects on survival of bobwhites from point feeders and food plots (Frye 1954, Robel et al. 1974, DeMaso et al. 1999, Guthery et al. 2004), supplemental feeding as defined in this study has been found to increase bobwhite survival rates (Sisson et al. 2000, Buckley et al. 2015). A 10-year study at Tall Timbers also measured greater annual survival in 9 of 10 years (Palmer and Wellendorf, unpublished data). Therefore, while not the primary focus of this study, a secondary interest was to determine whether supplemental feed would result in lower space use and movements as a mechanism for reduced predation and increased survival. Less time spent foraging by bobwhites could equate to lower movements and lower vulnerability to predation and harvest by increasing vigilance behaviors. Consistent with this idea, Sisson et al. (2000) observed smaller home ranges and more localized movements on fed sites. However, no studies have determined how supplemental feeding affects foraging behavior and daily movements which may indirectly influence survival rates.

To understand potential costs and benefits of supplemental feeding requires knowledge of how food resources influence individual behavior. Therefore, we examine effects of supplemental feeding on bobwhite behavior by determining temporal variation seed availability and its relationship to bobwhite diet, seasonal home ranges, space use, and daily movement of bobwhites. We hypothesized that as supplemental feed availability increased, bobwhite movements and daily and seasonal space use should decrease and that daily movements should be concentrated nearer to the feed patch, especially when supplemental food resources were abundant. Further we predicted that bobwhites would abandon supplemental food resources before they were entirely gone, indicating an empirical giving up density energy value for habitat on our study area.

STUDY AREA

Tall Timbers Research Station (TTRS 30.66° N, 84.22° W) is located in north Leon County, Florida in an area that is commonly referred to as "the Red Hills". Tall Timbers Research Station is ~1,570 ha in size. Most of the property (66%) was upland pine forests which consist of longleaf pine (*Pinus palustris*), loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) with a groundstory of warm season grasses, forbs, legumes and hardwood shrubs and resprouting tree species. Pine uplands are intermixed with hardwood drains (21%) and annually disked fallow fields (13%). Prescribed burning, mowing, and roller chopping are techniques frequently used at TTRS to reduce hardwood encroachment while maintaining diverse grass-forb-shrub ground cover vegetation suitable for bobwhite. Over 20 years of telemetry data demonstrate that 100% of the upland habitats on TTRS was used as habitat by bobwhites.

Climate is considered relatively moderate with mean annual temperatures ranging from 1-34 °C. Average humidity is 77.5%. Average rainfall is 145 cm with most rain falling between June and September. Average elevation at TTRS is 61 m.

METHODS

TTRS was divided into 3 study areas (244 ha, 242 ha, and 232 ha). Each year a feeding rate was assigned to an individual treatment area. Sorghum was used as the supplemental feed. Feed rate treatments consisted of a high rate of 174 L/ha/year (2.0 bushels/acre/year), a low rate of 44 L/ha/year (0.5 bushels/acre/year), and a zero feed rate in the control. These feeding treatments were applied to the study areas for one year. The high feed rate is similar to that used on managed quail lands in the region. We randomly assigned treatment and control during year one then treatment and control were rotated counter-clockwise in year two to minimize confounding study area with treatment.

Bobwhite were captured using baited walk-in funnel traps (Stoddard 1931). Traps were baited with sorghum and covered with recently cut pine boughs in an attempt to minimize stress of captured birds and to keep traps hidden from predators. Gender, age class, and weight for each captured bobwhite were recorded (Rosene 1969). Additionally, a uniquely numbered aluminum leg band was attached (National Band and Tag Co., Newport, KY). Bobwhite were then fitted with 6.4–6.9 g necklace radio transmitters (American Wildlife Enterprises, Monticello, FL). Trapping, handling, and marking procedures were consistent with the guidelines of the Tall Timbers Research, Inc. Institutional Animal Care and Use Committee Permit (IACUC no. GB2001-01).

Spreading Sorghum and Seed Loss Rates

Supplemental feed was distributed on a biweekly feeding schedule throughout the year. Supplemental feed was applied using John Deere 6400 tractor equipped with a 40 bushel 3-point spreader (Vicon Spreaders, Peach Bottom, PA, 17536) to half of the feeding trail on both feed treatments on the first day and then the remainder of the feed trail on both treatments on the second day.

Prior to conducting the feeding trials, we calibrated the spreader to distribute the low and high feeding rates and determine the distance distribution of seed thrown from the spreader. We did this by counting sorghum seeds collected in buckets placed at 0.91 m intervals perpendicular to the direction of the tractor and spreader until the correct gate settings on the spreader were determined. Once we determined the correct gate settings, we conducted 10 trials for each setting of the seed release gate to determine the number of seeds spread at different distances from the tractor. We determined that the spreader distributed seeds 7 m to either side of the centerline of the feed trail and defined this 14 m-wide swath as the ‘feed patch’ which covered about 11% of the total habitat within the low and high feed treatments based on the distance in each study area.

We determined sorghum availability through time by sampling sorghum in both treatments during February and March at 60 random points placed within the feed patch using Hawth’s tools (Hawth’s Analysis Tools for ArcGIS. Version 3.27 http://www.spatialecology.com/htools). Each point was flagged by placing pin flags at each of the four corners of a 0.5 m^2 plot. Preexisting sorghum seed was removed, along with debris, to the soil humus layer using a 5.5 hp wet-dry vacuum (Shop-Vac, Williamsport, PA) powered by a portable generator. Then a known number of seeds, specific to each feeding treatment as predetermined from spreader calibration, were hand deposited within each plot. We replaced debris collected by the vacuum back over the plot mimicking the surrounding environment. We counted residual seed availability within 20 of the 60 plots during 3 sampling periods on days 5, 10, 15, using the same vacuum system.

We estimated the relationship of seed abundance versus time data using Curve Expert 1.3 (CurveExpert software, http://www.curveexpert.net). We considered a set of models that included linear, exponential, power law, yield-density, and sigmoidal and selected best fit model based on largest coefficient of determination (r^2).

Diet

We determined diet of bobwhites harvested on the study area in February, 2009–2010. Hunting effort was not constant among study areas. Crops of harvested bobwhites were collected and time of harvest, date, feed treatment, and gender were recorded. Crop contents were removed and food items were dried to a constant mass in an industrial sized dryer set at 27 °C for 72 hours (Masters et al. 2007). Seed items were identified to lowest taxon possible using Tall Timbers Research Station reference seed collection, along with reference manuals by Martin and Barkley (1961). Whitelaw et al. (2009) provided comprehensive bobwhite diet data for TTRS on supplemental fed and control areas, therefore we presented percent (by dry weight) of sorghum and other seed types that made up a large proportion of the diet.

Daily Telemetry

During 1 February through 15 March 2009 and 2010, locations and daily movements of radio-marked bobwhites were monitored on average 4 times a week in a manner that coincided with the seed availability schedule. This resulted in an even distribution of samples throughout the two-week feeding cycle. A covey was chosen at random using a random number generator within each of the two feed treatments and these coveys were then located every 30 minutes diurnally. Coveys to be monitored were located on the roost the night prior to monitoring to minimize disturbance when first locating a covey pre-dawn the next monitoring (Kenward 2001). Observers maintained a distance of at least 40 m from the monitored coveys and were as quiet as possible in order to limit any potential influence on covey movements. Observers were trained to estimate distance through a combination of triangulation, homing, and signal strength. Using an orienteering compass, observers took bearings and estimated distances to covey locations, producing an average of 21 (17–24) locations/covey/day. Observers used GPS units that did not have the feed patch in the background to eliminate any potential bias for locations on or near the feed patch.

Observer locations were then georeferenced (+/- 1 m) using a differentially corrected Trimble Geoexplorer GPS unit and Pathfinder Software (Trimble Navigation Limited, Sunnyvale, CA). Covey locations were triangulated using a minimum of 3 positions within LOAS 4.0 software (Ecological Software Solutions LLC, Hegymagas, Hungary) using a maximum likelihood estimator. We censored locations with an error eclipse greater than 0.01 ha.

Seasonal Telemetry

Individual bobwhites in the low, high, and control treatments were located >3 times per week from 1 November to 15 March during both 2008–09 and 2009–10 winter seasons using homing techniques (Fuller et al. 2005). Locations were plotted on detailed aerial photos at a scale of 1:1000 in the field which were created in Arc Map and included land cover types as well as terrain features and transferred into a Geographical Information System ArcGIS 9.3 (ArcGIS, Version 9.3. Environmental Systems Research Institute, Redlands, California, USA) to determine spatial coordinates.

Telemetry locations were used to estimate daily and seasonal 95% utilization distributions of radio-marked bobwhite in relation to supplemental feed availability. We used daily telemetry locations for all radio-collared birds in the three treatments to estimate seasonal utilization distributions. We used intensive telemetry locations from bobwhite coveys to estimate daily utilization distributions. Utilization distributions as well as the smoothing parameter (h) were created using ADEHABITAT package in R (Calenge 2006). A smoothing parameter was created for ranges in each year of the study as the mean, least-squares cross-validation-derived h over all individuals where the algorithm converged (bivariate normal kernel; Kenward 2001, Terhune et al. 2010).

Area within 95% utility distributions were then calculated using X tools Pro extension in ArcGIS 9.3. An analysis of variance (ANOVA) within a general linear model (GLM) in SAS® software, Version 9.2 (SAS Institute, Cary, North Carolina, USA) was used to compare daily and seasonal ranges by treatment, year and year by treatment effects. Estimates were reported as least squared means and associated standard errors.

Proximity to Feed Patch

To determine if bobwhite selected locations closer to supplemental feed patch, we compared mean distance to feed patches between covey locations and an equal number of randomly generated locations. We generated an equal number of random locations using Hawth's tools within the treatment area used by each covey. We generated distances to the feed patch using the NEAR function in ArcGIS 9.3. Unless noted otherwise, all statistical analyses were conducted using SAS® software, Version 9.2 (SAS Institute, Cary, North Carolina, USA). An overall mean was determined for each radio-marked covey and paired random locations using PROC MEANS. Individual coveys were used as sampling unit (random effect) for an analysis of variance (ANOVA) within a mixed model.

We classified locations of coveys from intensive daily monitoring as in or out of feed patch in a binary fashion. We treated covey-days as independent sampling units and estimated the proportion of 30-minute relocations in feed patch for each covey-day. To determine if proportional use of feed patches was influenced by supplemental feed, we modeled probability of being in a patch using an events/trials (locations in feed patch/total number of locations in covey day) response in a logistic regression within PROC LOGISTIC.

We used multi-response permutation procedures (MRPP) to test for distributional differences between locations of bobwhite in low and high feeding treatments as it is possible for locational distributions to differ without influencing either mean daily movements, distance to feed lines, or range size. MRPP can be used to simultaneously test for distributional differences in central tendency and dispersion for univariate and multivariate analyses in a completely randomized one-way design (Cade and Richards, 2005). We used MRPP to test for differences between feed treatments in dispersion of daily locations within BLOSSOM version W2008.04.02 (Blossom Statistical Software. United States Geological Survey. Fort Collins Science Center. Fort Collins, Colorado, USA). We centered the daily locational data relative to the mean x and y coordinate for each individual covey, scaling all locations to a common origin. Having removed differences in central tendency through centering, subsequent MRPP test on the centered data then became a test of bivariate dispersion.

RESULTS

We sampled sorghum seed availability in 326 0.5 m^2 plots (164 high rate and 162 in the low rate) between 1 February 2009 and 15 March 2009 and 255 0.5 m^2 plots (125 high rate and 130 low rate) between 1 February 2010 and 15 March 2010. Seed depletion for the high feed treatment declined at 5-day intervals from 50 seeds to an average of 37, 24, and 12 and fit a linear model ($r^2 = 0.998$). Seed depletion for the low feed treatment declined at 5-day intervals from 11 seeds to an average of 5, 1 and 0 and followed a modified power function ($r^2 = 0.998$).

We harvested 285 bobwhites, with 122 in the high feed rate treatment, 102 in low feed rate treatment, and 61 in control. Mean crop weight did not differ significantly between years ($F_{1,279} = 2.34$, $P = 0.13$) or among feed treatments ($F_{2,279} = 1.90$, $P = 0.15$). Mean weight of crop

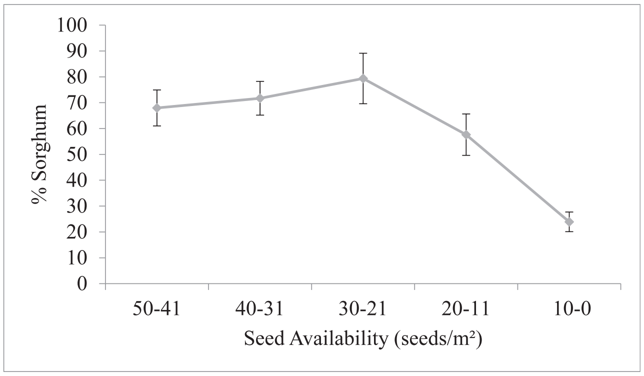

Fig. 1. Mean percentage of sorghum in northern bobwhite crops collected in February 2009 and 2010, at Tall Timbers Research Station, Leon Co, Florida, USA. Error bars indicate ± 1 standard error.

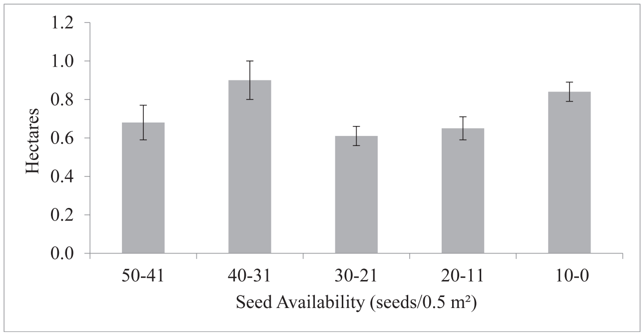

Fig. 2. Daily range sizes (ha) for radio-marked northern bobwhite coveys, in relation to daily sorghum seed availability, February and March, 2009 and 2010, at Tall Timbers Research Station, Leon Co., Florida, USA. Error bars indicate 1 standard error.

contents were 2.2 g and 2.4 g for high feed treatment in 2009 and 2010, 2.6 g and 2.8 g for low feed treatment in 2009 and 2010, and 2.3 g and 2.9 g for the control in 2009 and 2010. Crop contents of bobwhites harvested in the high feed treatment consisted of 74 % sorghum in 2009 and 95% sorghum in 2010. Crop contents of bobwhites harvested from the low feed treatment comprised of partridge pea (*Chamaecrista* spp.) (30%), sorghum (27%), acorn (*Quercus* spp.) mast (19%) in 2009, and partridge pea (40%), sorghum (29%), and acorn mast (0.2%) in 2010. Crop contents of birds harvested in the control treatment in 2009 were primarily comprised of partridge pea (49%) and acorn mast (25%). In 2010, crop contents from control feed treatment were predominantly partridge pea (65%) with less acorn (9%). At sorghum counts greater than 20 seeds / 0.5 m^2, sorghum comprised 68.0 % (SE = 6.96) to 79.4 % (SE = 8.01) of crop contents, declining to 57.6 % (SE = 8.01), when sorghum availability was between 11 and 20 seeds / 0.5 m^2 and 23.9 % (SE = 3.8) at 10 seeds / 0.5 m^2 or less (Figure 1).

Winter seasonal range sizes of coveys did not differ significantly among feeding levels ($F_{2,83} = 0.60$ $P = 0.55$) or between years ($F_{1,83} = 1.29$ $P = 0.25$). During 2009, mean winter range sizes of 37 coveys were 18.03 ha (SE = 1.24) in high feed treatment, 18.6 ha (SE = 1.77) in low feed treatment and 18.7 ha (SE = 1.75) for control treatment. In 2010, mean winter range sizes of 52 coveys were 18.3 ha (SE = 1.18), 20.4 ha (SE = 1.19) and 21.2 ha (SE = 2.53) for high, low, and control treatments, respectively.

Daily range size ($n = 107$ coveys) were slightly lower for coveys in high feed rate treatments ($F_{1,103} = 3.47$ $P = 0.06$) with no difference among years ($F_{1,103} = 0.07$ $P = 0.79$). In 2009, mean daily ranges were 0.72 ha (SE = 0.06) in high feed treatment and 0.85 ha (SE = 0.06) for low feed treatment and in 2010 mean daily ranges were 0.71 ha (SE = 0.06) and 0.83 ha (SE = 0.08) for the high and low feed rate treatments, respectively. Mean daily range sizes, grouped by seed availability classes, had overlapping confidence intervals and as such did not differ substantively (Figure 2).

Bobwhite traveled a mean 25.2 m (SE = 0.65) between consecutive locations during daily intensive focal periods. Mean step length between consecutive locations did not differ between feeding treatments ($F_{1,2178} = 0.99$, $P = 0.32$) or years ($F_{1,2178} = 0.81$, $P = 0.36$). During 2009, mean step lengths were 24.5 m (SE = 1.19) and 27.2 m (SE = 1.53) for high and low feed treatments, respectively. In 2010, the mean step lengths were 24.8 m (SE = 1.29) and 24.6 m (SE = 1.2) for high and low feed treatments, respectively.

Similarly, total distance that bobwhite coveys traveled throughout the day did not differ between treatments ($F_{1,103} = 0.17$, $P = 0.68$) or years ($F_{1,103} < 0.01$, $P = 0.95$). In 2009 total distance traveled over the entire day was 495.8 m (SE = 33.04) for the high feed treatment and 528.3 m (SE = 33.01) for the low feed treatment. In 2010, bobwhites total travel distance of 514.9 m (SE = 39.2) for the high feed treatment and 513.5 m (SE = 40.99) for the low feed treatment.

Centered bivariate locational distributions were different among feed rates ($P < 0.001$). Mean Euclidian distance between all pairwise combinations of centered locations in high feed treatment (D = 1.43 m) was 23% lower than in the low feed treatment (D = 1.75 m) indicating greater dispersion in the low feed treatment.

We used telemetry locations from 38 intensively monitored bobwhite, 16 in 2009 and 22 in 2010, to examine proximity of daily locations to the feed patch. The mean distance to feed patch was 42.0 m (SE = 1.0) and 41.3 m (SE = 3.15) for random and actual covey locations, respectively ($F_{1,71} = 0.04$, $P = 0.83$). Mean distance to feed patch did not differ significantly between treatments ($F_{1,71} = 0.43$, $P = 0.52$), or years ($F_{1,71} = 0.27$, $P = 0.60$). While mean distances over the 15-day feeding period did not differ from random, coveys tended to choose locations closer to feed line as seed availability decreased from 40 to 11 seeds / 0.5 m^2, reaching a minimum distance of 26.6 m (SE = 6.07) at about 11 seeds. This decreasing trend was followed by an increase in the mean distance to feed line to 40.4 m (SE = 3.17) when seed availability decreased below 10 seeds (Figure 3) which corresponded to a reduction in sorghum in bobwhite diets.

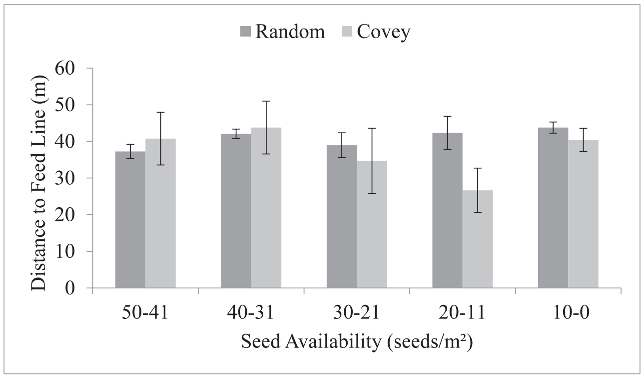

Fig. 3. Mean distance to feed line for radio-marked northern bobwhite coveys and randomly-generated locations, February 2009 and 2010, at Tall Timbers Research Station, Leon Co., Florida, USA. Error bars indicate 1 standard error.

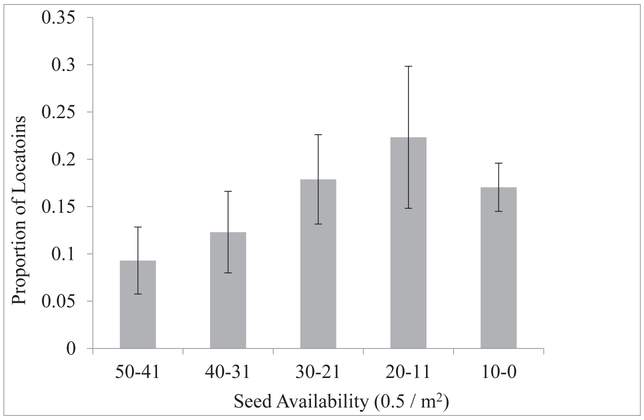

Fig. 4. Mean proportion of covey locations within feed patch, February 2009 and 2010, at Tall Timbers Research Station, Leon Co., Florida, USA. Error bars indicate 1 standard error.

We used locations from 102 covey/days to estimate proportion of time within feed patch. Mean number of locations per covey/day was 20.8 (SD = 2.2). Proportion of daily locations within feed patch (9–22%) varied in relation to seed availability (Figure 4). The model that best explained proportional use of feed patches included seed availability and seed availability squared. At 40 to 50 seeds / 0.5 m^2, approximately 9% of locations were within the feed patch, increasing to 22% at 10 to 20 seeds / 0.5 m^2 then declining to slightly to 17% at 1 to 10 seeds / 0.5 m^2 .

DISCUSSION

We designed our feeding rates so that bobwhites experienced a range from abundant sorghum availability commonly spread on wild bobwhite properties to none through each 15-day feeding period. Sorghum spread at the high rate declined monotonically to a starting level of the low rate and provided us an opportunity to observe bobwhite behavior along a continuum of food availability. Sorghum spread at the low rate declined to zero and was no longer available to bobwhites after about 10 days. We could not find previous studies on depletion of supplemental feed spread in an upland pine ecosystem; however, research in Tennessee characterized loss of agricultural seeds in fields after harvest using an exponential decay function yielded similar results to this study (Foster et al. 2010).

As predicted by OFT, when supplemental feed was abundantly available, bobwhite selected for sorghum over less profitable native seeds and greens. Use of the feed patch by bobwhites varied slightly in relation to seed availability however patterns in their movements and diet in relation to seed availability suggested a giving up density at which bobwhites choose native seeds over sorghum. At higher feed densities (30–50 seeds / 0.5 m^2) bobwhites apparently fed quickly and left the feed patch. This is supported by observed high amounts of sorghum in the diet and low use of the feed patch (e.g., shorter foraging effort); thus resulting in similar distances to random points from the feed patch as bobwhites travelled through other parts of their home range. Use of sorghum in their diet remained high (> 85%) until seeds declined to 10–21 seeds / m^2. At this density of seeds, bobwhite locations were 33% closer to the feed patch, than at higher densities and the proportion of their daily range in the feed patch was highest. This suggests that bobwhites were increasing foraging time for sorghum as seed availability declined. At <10 seeds / m^2 bobwhites diet shifted to primarily native foods and distance to, and locations within, the feed patch was similar to higher seed densities, however, for different reasons. At this point, bobwhite reduced foraging time in the feed patch which suggests at approximately <15 seeds / 0.5 m^2 energy gained within that feed patch is equal to or falls below that of the surrounding habitat. This diet switching follows predictions of the marginal value theorem (Charnov 1976) and suggested a foraging threshold at this time of year was ~15 sorghum seeds and ~1.6 kcals / 0.5 m^2 (Robel et al. 1974). Miller (2011) found similar levels of metabolizable energy in the crops of bobwhites harvested in this study (8.39 kcals) among high, low, and control treatments. He also reported little difference among treatments in whole body lipid levels, although lipid levels were significantly greater in the high feed rate treatment in 2010 when acorn mast was less available. Given adequate energy is available in native seeds bobwhites could choose to forage exclusively on native seed sources. That they chose a higher energy seed relative to native foods, suggests bobwhites selected the sorghum over native seeds to minimize foraging time (Schoener 1971, Charnov 1976). By minimizing foraging time, bobwhites may be able to increase time spent in habitats with better thermoregulatory or predator avoidance qualities (Lima 1985), thus improving their fitness

Seasonal range sizes were similar among feeding rates. Similarly, total daily movements and distance moved between locations was not affected by the presence of the feed patch. This suggests that despite a well dispersed feed patch system, bobwhite coveys moved to meet other behavioral needs, such as predator avoidance and thermoregulation. Buckley et al. (2015) also found no difference in winter home range size of bobwhites with access to supplemental feed. Sisson et al.

(2000) observed smaller winter ranges on fed versus unfed sites. Their study occurred on a property with lower soil fertility and less native food than our study site; thus their bobwhite may have had to move greater distances to find feed patches that minimized foraging time.

Some studies have documented increased survival rates for bobwhites provided with a well-dispersed feeding line system such as the program used in this study (Sisson et al. 2000, Buckley et al. 2015). While bobwhites used the feed patch, they did not significantly alter their daily and seasonal use patterns. We hypothesized that bobwhites with access to super abundant, high energy foods, would move significantly less and reduced movements may be a mechanism for predator avoidance and reduced predation. Because bobwhites moved similarly among treatments suggests that other factors, such as increased buffer prey as a result of supplemental feeding (Doonan and Slade 1995), may be a more important mechanism to reduce predation. In more northerly climates, access to high energy foods during periods of severe weather is a nutritional mechanism for increasing bobwhite survival (Buckley et al. 2015, Janke et al. 2015). Severe winter weather is not an issue for survival of bobwhites in sub-tropical regions (Stoddard 1931, Terhune et al. 2007). This suggests that increased survival rates from supplemental feeding observed in southern latitudes may largely be a result of indirect mechanisms.

Unlike point feeders that may concentrate bobwhites, sorghum was well dispersed across our study site, covering 11% of the habitat area throughout the pine uplands. Applying supplemental feed by this method does not concentrate coveys because they were not disproportionally selecting locations close to the feed line, or spending more time in or near the feed patch than spatially-available. Well-dispersed feed lines allow individuals to forage without increasing the likelihood of directly contacting other individuals. It also permits individuals to choose suitable portions of the feed patch that are associated with suitable habitat to match changing conditions. In these manners, chances of disease transmission or predation as compared to stationary wildlife feeders (The Wildlife Society 2006) is mitigated.

Over the feeding cycle and in both the high and low feeding treatments, bobwhites were not closer to feed patches than random. This is likely because the continuous feed patch winding through the habitat permits bobwhites to forage more or less naturally. This is different from systems such as point feeders or feeding along roads which are not designed to reach the home ranges of each covey on an area in many different locations (Lehman 1984, Boyer 1989, Haines et al. 2004). Sisson et al. (2000) used a similar supplemental feeding system in their study and found no evidence of increased harvest for bobwhites on the fed area versus the unfed area. While bobwhites used the feed patch, their limited association with it suggests that broadcasting supplemental feed would not serve as "baiting" coveys such as found with point feeding systems (DeMaso et al. 1999). However, the lack of bobwhites association with a feeding patch may depend on how the distribution of feed patches on the landscape. Research that compares bobwhite space use and harvest at a range of feed patch densities may better address at what point supplemental feed would concentrate bobwhites around a feed patch and increase susceptibility to harvest.

MANAGEMENT RECOMMENDATIONS

If supplemental feeding programs are used, we suggest feeding at the rate of 2.0 bushels per acre of habitat per year to allow bobwhites access to high energy foods at all times during the feeding cycle. We suggest that by distributing feed across the landscape, rather than at point feeders, limits the potential for baiting bobwhites to a specific location potentially increasing harvest rate. This study underscores the importance of managing for diverse native food sources, including mast producing overstory, especially when supplemental feeding is depleted or not used. Hunting along a supplemental feeding patch is likely to be unproductive as bobwhites spend only a small proportion of their day associated with it.

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NORTHERN BOBWHITE HOME RANGE SIZES AND MOVEMENTS IN SOUTH TEXAS

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ABSTRACT

Northern bobwhites (*Colinus virginianus*) often have relatively small home ranges (<1-km radius); however, occasional long-distance movements also have been recorded, which may help maintain connectivity and genetic diversity within and among populations. We quantified movements of radiocollared northern bobwhites on the King Ranch in South Texas, USA. For each bird we determined core area, home range (fixed kernel), mean movement rate, and maximum distance moved. We compared movements across age, gender, precipitation trends, and plant communities using Mann–Whitney U and Kruskal–Wallis tests. Almost half (44.7%) of the birds moved >400 m (max. distance moved) and 46 (16%) moved >1 km over the course of the study. Males had higher movement rates (juvenile $\bar{x} = 54.9$ m, SE $= 1.77$ m, $n = 64$; adult $\bar{x} = 56.6$ m, SE $= 1.95$ m, $n = 65$) than females (juvenile $\bar{x} = 51.26$ m, SE $= 1.80$ m, $n = 102$; adult $\bar{x} = 48.14$ m, SE $= 1.49$ m, $n = 62$; $\chi^2_{3,289} = 14.90$, $P = 0.02$). Maximum distance moved was longer in dry years (609.8 ± 136.3 m) compared with normal or moist years ($\bar{x} = 542.8$ m, SE $= 47.0$ m; $\bar{x} = 536.6$ m, SE $= 28.8$ m, respectively, $n = 293$). Northern bobwhites moved farther in dry years, possibly to find cover and food. A small percentage made relatively long-distance movements ($n = 18$, 6%, >1.6 km, max. 6.5 km). These rare movements may influence gene flow and genetic structure of northern bobwhite populations in South Texas.

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Animal movements may be driven by competition for resources, competition for mates, and landscapes that lack necessary vegetation composition and/or patch sizes. Gene flow may improve genetic diversity if dispersers survive to reproduce in a new population. Conversely, reduced gene flow may result in lower genetic diversity if a species' movement is limited (e.g., blue ducks (*Hymenolaimus malacorhynchos;* Triggs et al. 1992). Recurring fluctuations in populations with limited dispersal may act as small genetic bottlenecks. These populations may lose genetic diversity through genetic drift during phases of low population density (Nei et al. 1975). Bottlenecks and isolation can lead to large genetic variation among populations facing habitat fragmentation (e.g., eastern wild turkeys [*Meleagris gallopavo silvestri*]; Leberg 1991).

Most northern bobwhites (*Colinus virginianus*) have small home ranges (<30 ha; Yoho and Dimmick 1972, DeVos and Mueller 1993, Janke and Gates 2013) and are often found within 10 km of their original banding location (Stoddard 1931, Murphy and Baskett 1952, Smith et al. 1982, Lehmann 1984). Occasionally, northern bobwhites are capable of long-distance movements, sometimes travelling >100 km (Cooke 1946, Kiel 1976, Lehmann 1984:119). Research from the Caesar Kleberg Wildlife Research Institute indicates a weak genetic

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structure ($\theta_{ST} = 0.037$, Wehland 2006; $F_{ST} = 0.015$, Miller 2014) for northern bobwhite populations in South Texas, USA. Gene flow, dispersal, or other factors may drive this weak genetic structure; thus, it is important to assess which factors compel northern bobwhites to move long distances.

Northern bobwhite reproduction and extreme population fluctuations are tied to rainfall (Bridges et al. 2001, Hernández and Peterson 2007, Rader et al. 2007, Tri et al. 2012) in South Texas. Herbaceous vegetation may be limited during years with below-average rainfall, forcing northern bobwhites to move farther in search of resources or potentially face local population declines (Peterson 2001). Thus, precipitation and temperature may affect availability of food and cover, movement, and gene flow of northern bobwhite populations.

Northern bobwhite behavior and abundance may also drive movement. In the autumn, northern bobwhite family groups may merge into one covey or break into separate coveys. This behavior is known as the covey shuffle (Lehmann 1984). Winter coveys may provide a source of mates in the spring. However, some birds must move farther in search of mates when coveys have uneven sex ratios and exhibit agonistic behavior (Lehmann 1984:50). Population density may also be a factor; Rosene (1969:80) recounted a mass movement of northern bobwhites on the Mississippi and Ohio riverbanks in the 1930s. These birds may have been attempting to move from populations of high density to those of lower density (Rosene 1969).

Whether rainfall or northern bobwhite behavior drives individual birds to disperse, there may be a gender or age bias to movement. Female-biased dispersal occurs in bird species, most likely because males defend the territories and females choose males based on territory quality. Among galliforms, female-biased dispersal has been documented in blue grouse (*Dendragapus obscurus;* Jamieson and Zwickel 1983), ruffed grouse (*Bonasa umbellus;* Small and Rusch 1989), and western capercaillie (*Tetrao urogallus;* Segelbacher et al. 2008). However, northern bobwhite dispersal appears slightly biased toward males (Stoddard 1931, Townsend et al. 2003). Age may be another potential bias; juveniles appear to disperse farther than adults (Smith et al. 1982, Townsend et al. 2003).

Previous research by the Caesar Kleberg Wildlife Research Institute provided an opportunity to study home ranges and movements of a northern bobwhite population in South Texas over a 7-year period (Rusk et al. 2006, Arredondo et al. 2007, DeMaso 2008). We compared core area, home range size, and movements of northern bobwhites across age and gender groups, varying annual and seasonal weather conditions, and land cover types that may influence home range and movement.

We tested 3 hypotheses to understand effects of age and gender, weather, and weather and plant community. Our first hypothesis was that juvenile males would have larger home ranges and longer movements, compared with females or adult males, than would be expected by chance. Our second hypothesis was that northern bobwhites would be more likely to disperse during dry years when food and cover may be limited. Our third hypothesis focused on weather and plant communities. We hypothesized that home ranges would encompass both grassland and mesquite-shrubland (*Prosopis glandulosa*) during years with normal precipitation as birds moved between feeding and loafing cover, compared with dry years when availability of grassland cover was more limited. In dry years we expected home ranges to be more frequently located in mesquite-shrubland.

STUDY AREA

Our study was conducted on the King Ranch, a private ranch in South Texas with mesquite shrubland throughout the property. The King Ranch covers 333,866 ha in portions of Brooks, Kleberg, and Kenedy counties with small portions in Jim Wells, Nueces, and Willacy counties. The ranch was managed for cattle grazing, oil and gas development, and hunting for large ungulates (e.g., white-tailed deer [*Odocoileus virginianus*]) and game birds, including northern bobwhite (Ashton and Sneed 2010).

Biologists collected data for this study from the Encino division of the King Ranch in Brooks County. Biologists sampled 3 pastures as spatially independent units: North Viboras (1,966 ha), Loba (1,379 ha), and Cuates (1,240 ha). A north–south gradient of woody cover increased from Cuates (10% cover) and Loba (~25% cover) to North Viboras (>30% cover; Rusk et al. 2006). Dominant brush species that provided woody cover included honey mesquite, granjeño (*Celtis pallida*), huisache (*Vachellia farnesiana farnesiana*), live oak (*Quercus virginiana*), and prickly pear cactus (*Opuntia engelmannii lindheimeri*). Croton (*Croton* sp.), sunflower (*Helianthus annuus*), dayflower (*Commelina erecta*), and partridge pea (*Chamaecrista fasciculata*) were common forbs (Hernández et al. 2002). Grasses included little bluestem (*Schizachyrium scoparium*), paspalum (*Paspalum* sp.), threeawn (*Aristida* sp.), gulf cordgrass (*Spartina spartinae*), King Ranch bluestem (*Bothriochloa ischaemum*), sandbur (*Cenchrus incertus*), and buffelgrass (*Cenchrus ciliaris;* Hernández et al. 2002). The ranch had a semiarid climate with mean January temperature of 9° C and mean July temperature of 35° C. Mean annual rainfall was 56–66 cm with periods of drought (Rader et al. 2007). Droughts occurred approximately every 4–5 years during the course of the study.

METHODS

Northern Bobwhite Movements

Biologists trapped >2,000 northern bobwhites (DeMaso 2008) for the South Texas Quail Research Project from January through December of 1998–2008. They trapped birds using standard funnel traps (Stoddard 1931:442) and night-netting (Labisky 1968), fitted birds with an aluminum leg band, and then aged and sexed them (Rosene 1969). Biologists affixed a neck-loop radio-transmitter (Shields et al. 1982; American Wildlife Enterprises, Tallahassee, FL, USA) to birds weighing

>150 g. Birds weighing <150 g (transmitter >5% of bird's mass) were not radiomarked to limit potential effects of transmitters on northern bobwhite movement (Guthery and Lusk 2004). Handling procedures followed the protocols of the Texas A&M University-Kingsville Institutional Animal Care and Use Committee, permit 2003-3-3. Biologists determined locations of radiomarked northern bobwhites 3 times/week (DeMaso 2008) and all times of day to minimize diurnal peaks in activity. Triangulated locations were accurate to approximately 3 m (F. Hernández, Caesar Kleberg Wildlife Research Institute, Texas A&M - Kingsville, unpublished data). Biologists attempted to locate missing birds via fixed-wing aircraft after contact was lost with >5 birds (for cost-efficiency).

We used a subset from the data set (2000–2006) to determine northern bobwhite home range and movement. We eliminated locations where birds were found depredated because predators could have potentially moved the bird or the transmitter (Terhune et al. 2006). We then eliminated any bird with <20 locations (Haines et al. 2006, Brooke et al. 2015, Peters et al. 2015). We used the fixed-kernel method to determine core area and home ranges (Worton 1989) with a bandwidth of 100 m in ArcGIS (v. 10.1; ESRI, Inc. 2012, Redlands, CA, USA). The kernel density tool fits a curved surface over each point with a quadratic kernel function (Formula 4.5; Silverman 1986:76). Home ranges were defined as 100% kernels, and core areas were defined as the 50% density contour.

We determined linear movements for each bird, both mean movement rate and maximum distance moved. First we determined the distance between 2 consecutive locations and the number of days that elapsed between successive locations. We determined an index of mean movement rate, dividing the distance by the number of days and then averaging these values for each bird. Most (96%) successive locations occurred within 2 weeks. We removed all locations taken >1 week apart prior to determining mean weekly movement rates. We determined the maximum distance moved by each bird over the course of the study as the longest movement between 2 consecutive locations for that individual.

We measured the effect of rainfall on annual home ranges and movements with Palmer Modified Drought Index (PMDI) values (National Oceanic and Atmospheric Administration; http://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers.php). We classified years as dry (PMDI <–2.0), normal (PMDI = –1.99–1.99), or moist (PMDI >2.0). We then calculated annual core areas, home ranges, and movement distances as above. We grouped northern bobwhite data into dry, normal, and moist years and into 2 seasons to measure effects of rainfall during breeding (1 Mar–30 Aug) and nonbreeding (1 Nov–28 Feb) seasons. We analyzed effects of age and sex, rainfall, or weather on home ranges and movements during the autumn shuffle period (1 Sep–31 Oct) because of the limited sample of birds with an adequate number of locations available to calculate home range and core area.

We measured the combined effect of rainfall and plant community type on northern bobwhite movements. For rainfall we used Palmer Modified Drought Indices and for plant communities we used the Texas Ecological Land Classification Project (Phase IV) developed by the Missouri Resource Assessment Partnership and Texas Parks and Wildlife Department. This map was developed using ecoregions, Soil Survey Geographic database, digital elevation model variables, hydrology, vegetation information, and ecological processes (fire, grazing, flooding, etc.), together with ground-truthing. Several plant communities occurred in the study area. Sandy mesquite savanna was characterized by grasses (little bluestem, coastal bermudagrass [*Cynodon dactylon*], Lehmann lovegrass [*Eragrostis lehmanniana*]). Deep sand grasslands were defined by gulfdune paspalum (*Paspalum monostachyum*), tanglehead (*Heteropogon contortus*), camphor weed (*Heterotheca subaxillaris*), partridge pea, and a smaller proportion of woody species (Baccharis [*Baccharis* spp.], prickly pear cactus, small honey mesquite). Salty prairie consisted of gulf cordgrass (Elliott 2011). We determined the plant community for each home range and core area if >50% of the area fell within the community type.

Statistical Analyses

All data failed tests for a normal distribution; therefore, we compared core areas, home ranges, mean movement rate, and maximum distance moved to northern bobwhite age, sex, weather, and plant community effects using Kruskal–Wallis tests. We conducted statistical tests with the R v. 3.3.1 statistical software (R Core Team 2016).

RESULTS

We estimated core areas, home ranges, and movements from 293 northern bobwhites. Mean core area was 3.40 ha (SE = 0.09 ha). Mean home range was 14.76 ha (SE = 0.36 ha). Mean movement rate was 52.54 m (SE = 0.87 m). Maximum distance moved was 666.23 m (SE = 36.91 m). Almost half (n = 131, 44.7%) of the northern bobwhites moved >400 m (one-quarter mile). Only 18 (6%) northern bobwhites moved >1.6 km. The longest distance moved between successive radiolocations (6.5 km) was by a second-year female banded near Cuates and found 52 days later at a nest with 12 eggs, in Loba.

Age, Gender, and Pasture Effects

Core area, home range, and maximum distance moved did not differ significantly across age and gender (Fig. 1). Adult females had lower movement rates ($\bar{x}$ = 48.14, SE = 1.49, n = 62) than juvenile females ($\bar{x}$ = 51.26, SE = 1.58, n = 102), juvenile males ($\bar{x}$ = 54.95, SE = 1.77, n = 64), or adult males ($\bar{x}$ = 56.36, SE = 1.95, n = 65; $\chi^2_{3,\ 289}$ = 14.90, P = 0.002; Fig. 1). Among the 18 birds that moved >1.6 km during the study (Fig. 2), movement rates did not differ among juvenile males,

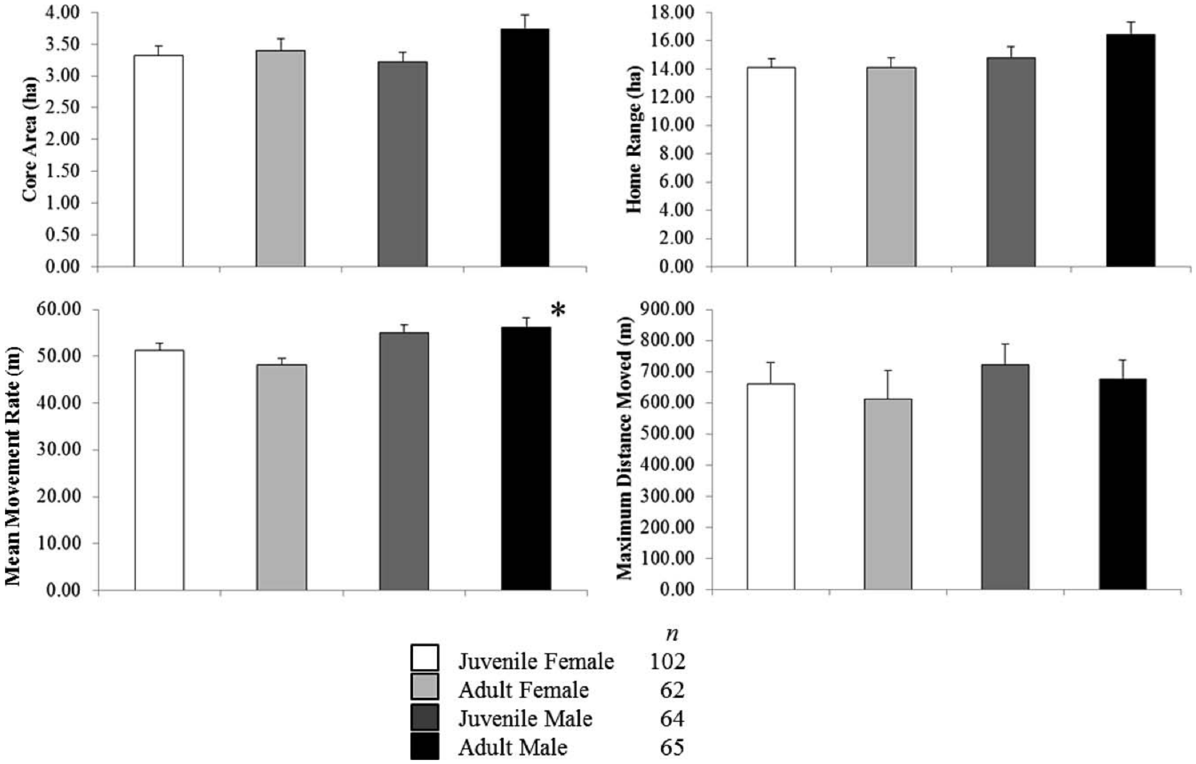

Fig. 1. Core area (ha), home range (ha), mean movement rate (m), and maximum distance moved (m) for northern bobwhites (*Colinus virginianus*) on the Encino Division of the King Ranch, South Texas, USA, during 2000–2006. Asterisk (*) denotes significant differences across age and gender, $\alpha = 0.05$. Error bars are standard error.

juvenile females, or adult males ($\chi^2_{2,\ 15} = 2.81$, $P = 0.246$). Only 3 of the 18 birds (17%) were adult females.

Mean movement rate differed across age, gender, and pasture ($\chi^2_{3,\ 289} = 25.16$, $P = 0.009$; Fig. 3). Mean movement rate for juvenile females, adult females, and juvenile males decreased as woody cover increased from Cuates to North Viboras. Females in North Viboras had lower movement rates compared with birds

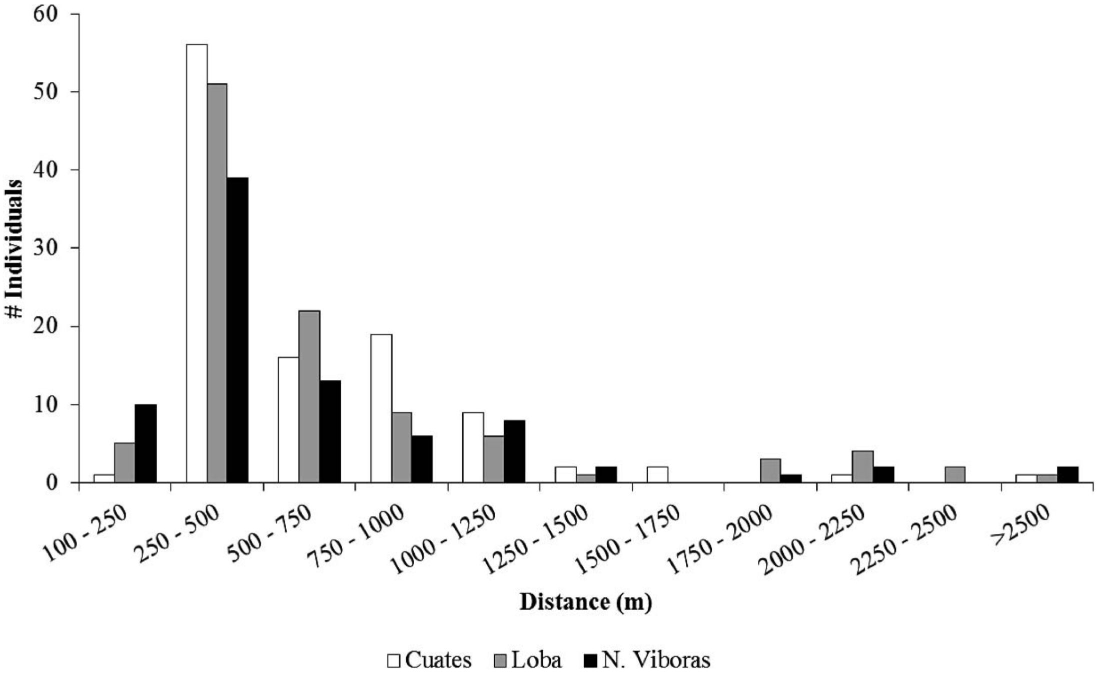

Fig. 2. Maximum distances (m) between consecutive radiolocations of northern bobwhites (*Colinus virginianus*) on the Encino Division of the King Ranch, South Texas, USA, during 2000–2006.

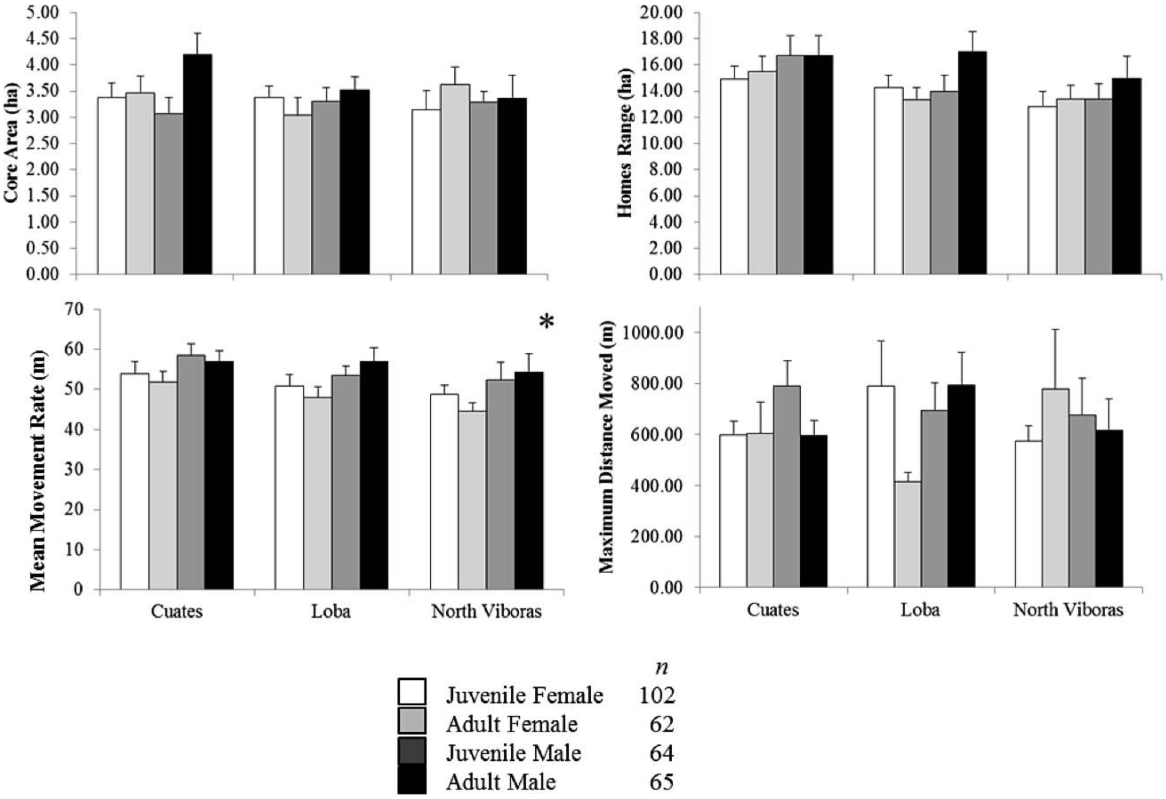

Fig. 3. Core area (ha), home range (ha), mean movement rate (m), and maximum distance moved (m) for northern bobwhites (*Colinus virginianus*) in 3 pastures on the Encino Division of the King Ranch, South Texas, USA, during 2000–2006. Asterisk (*) denotes significant differences across age, gender, and pasture, $\alpha = 0.05$. Error bars are standard error.

in other pastures and with males within North Viboras (Fig. 3).

Weather Effects

Mean home-range size was larger in normal years ($\bar{x} = 16.17$ ha, SE $= 0.58$ ha, $n = 124$) than in moist years ($\bar{x} = 12.68$ ha, SE $= 0.31$ ha, $n = 195$; W 193 $= 8{,}199$, $P < 0.001$; Fig. 4). Mean movement rates were similar in normal and moist years, but longer during dry years ($\chi^2_{2,\ 450} = 6.11$, $P = 0.047$). Northern bobwhites moved greater maximum distances in dry years ($\chi^2_{2,\ 450} = 7.35$, $P = 0.025$; Fig. 4).

Core area, home range, mean movement rate, and maximum distance moved differed across seasons and PMDI categories (Fig. 5). Home range was largest in normal summers ($\chi^2_{2,\ 308} = 39.47$, $P < 0.001$; Fig. 5). Movement rates were shortest in moist winters ($\chi^2_{2,\ 308} = 12.67$, $P = 0.005$). Maximum distance moved was also shortest in moist winters ($\chi^2_{2,\ 308} = 7.23$, $P = 0.027$; Fig. 5).

Weather and Plant Community Effects

Northern bobwhites occurred in all 3 plant communities defined by the Texas Vegetation Classification Project (Elliott 2011). Almost half ($n = 140$, 48%) were in sandy mesquite savanna. Another 98 (33%) were in deep sand grasslands. The remaining 56 home ranges (19%) were located in salty prairie.

Home range and maximum distance moved differed among normal and moist years and plant communities. Home ranges were larger in normal years and smaller in moist years ($\chi^2_{5,\ 311} = 12.53$, $P = 0.028$; Fig. 6). Maximum distances moved were shorter in salty prairie in normal years ($\chi^2_{5,\ 439} = 15.28$, $P = 0.009$). No birds were found in deep sand grassland in dry years.

DISCUSSION

Northern Bobwhite Age, Gender, and Pasture Effects

We expected that northern bobwhite juvenile males would have larger home ranges and longer movement rates and maximum distances moved compared with females and adult males, based on previous observations (Stoddard 1931, Smith et al. 1982, Fies et al. 2002, Cook et al. 2006). Juveniles have been shown to have longer movements. For example, Fies et al. (2002) and Cook et al. (2006) found that juveniles were more likely than adults to make long-distance movements in the spring and summer. Males also tend to make longer movements (Stoddard 1931, Terhune et al. 2010, and Liberati and Gates 2012) as well as possess larger home ranges (Urban 1972, West et al. 2012). Therefore, the fact that adult males in our study had shorter movements but larger

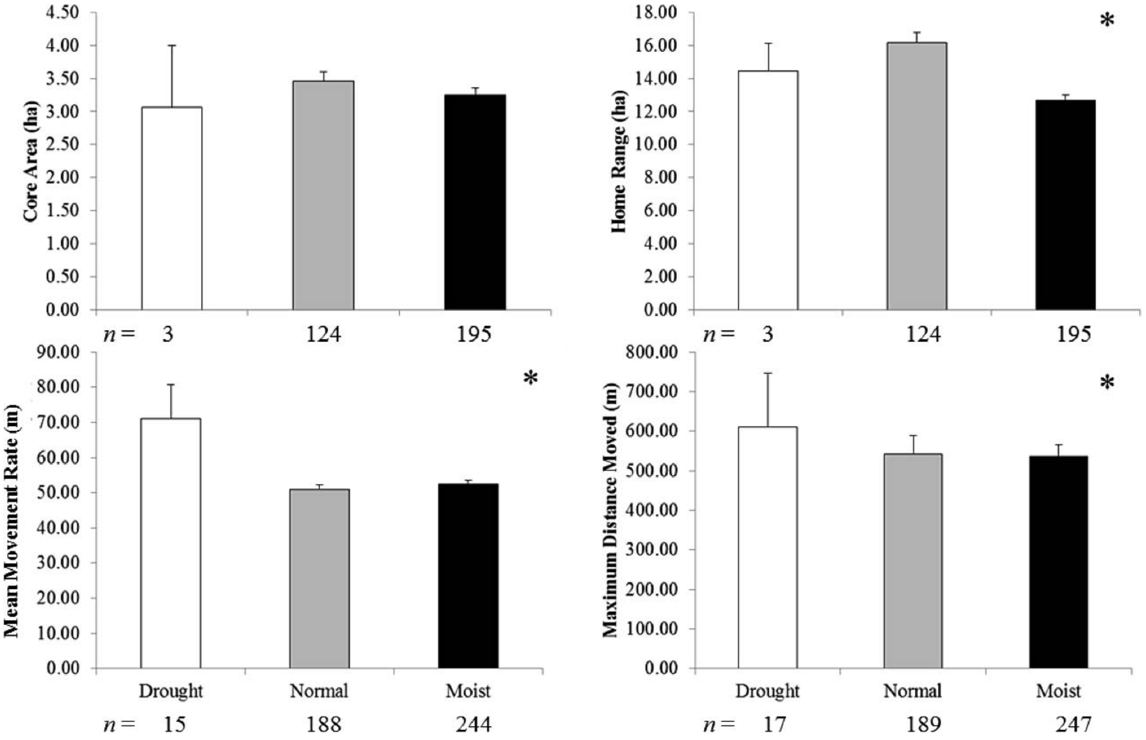

Fig. 4. Core area (ha), home range (ha), mean movement rate (m), and maximum distance moved (m) for northern bobwhites (*Colinus virginianus*) on the Encino Division of the King Ranch, South Texas, USA, during 2000–2006. We did not include data from drought years in our statistical tests for core area and home range because of the small sample size. Asterisk (*) denotes significant differences across dry (Palmer Modified Drought Index [PMDI], <–2.0), normal (PMDI = –1.99–1.99), and moist (PMDI >2.0) years, $\alpha = 0.05$. Error bars are standard error.

home ranges compared with juvenile males is interesting. It is possible that unpaired adult males in our study expanded home ranges as they searched for mates, similar to Urban (1972).

As expected, adult females in our study had the lowest mean movement rate. Adult females tend their nests and then make short movements with offspring. As offspring develop, females tend to make longer movements (Urban 1972, Taylor et al. 2000) and establish larger home ranges (Urban 1972, DeVos and Mueller 1993). Taylor et al. (2000) found that mean movement per day for incubating females averaged 357 m (SE = 54 m). However, mean movement per day increased to 503 m (SE = 60 m), once chicks fledged. Similarly, DeVos and Mueller (1993) found that northern bobwhite home ranges at Tall Timbers Research Station averaged 6.5 ha in the first 2 weeks posthatching and increased to 10 ha by the end of the first month.

Female northern bobwhites can and do move long distances. Fies et al. (2002) found that females moved farther ($\bar{x} = 1{,}328$ m, SE = 187 m) than males ($\bar{x} = 1{,}068$ m, SE = 100 m) in summer. Similarly, Cook et al. (2006) found that females made longer movements than males (F: $\bar{x} = 2{,}173$ m, SE = 319 m; M: $\bar{x} = 1{,}576$ m, SE = 230 m). The longest distance moved by a northern bobwhite in our study was by a second-year female (6.6 km). It is unclear whether she had a nest that failed prior to movement but that may be one impetus for female long-distance movement. Urban (1972) found that a hen in Illinois moved >2 km after her nest was destroyed.

Regardless of age, gender, or pasture, northern bobwhite movement rates were <65 m and mean maximum distances moved were <1 km (Fig. 3). Northern bobwhite movements are typically short (<8 km, Kiel 1976; <1.6 km, Lehmann 1984). It is possible that short daily movements in our study were due to the contiguous landscape that benefits northern bobwhite populations in South Texas.

Weather Effects

Weather has a significant effect on northern bobwhite populations in South Texas. Tri et al. (2012) found that variation in northern bobwhite age ratios could be attributed to rainfall ($r^2 = 0.94$). With adequate rainfall there should be sufficient food and nesting cover, which improves nest survival and should reduce the need for long-distance movements. In our study, northern bobwhites had larger home ranges in normal years compared with moist years and longer movement rates and maximum distances moved in drought years. This pattern held consistent over seasons (normal and moist summers, moist winters) as well.

Previous research on northern bobwhite movements and precipitation has found shifts in home range size (DeVos and Mueller 1993, West et al. 2012) and movements (Liberati and Gates 2012) with precipitation.

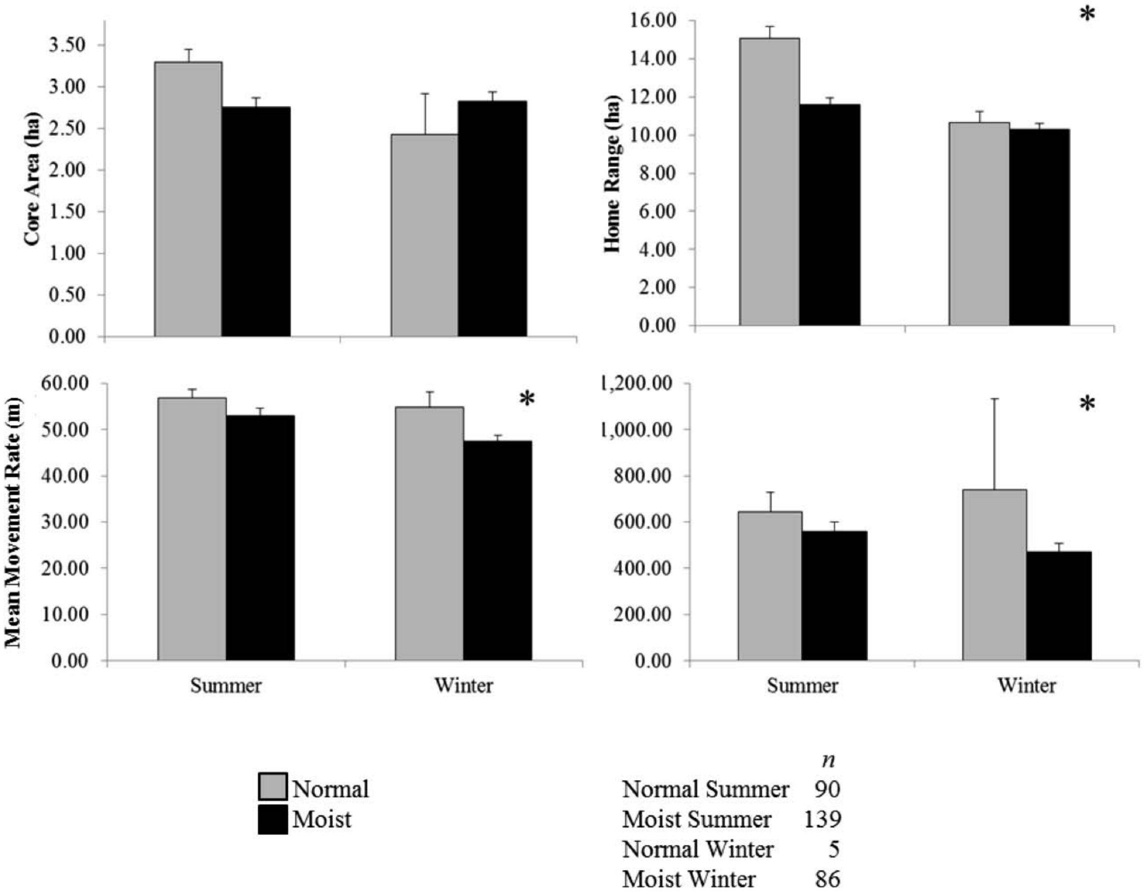

Fig. 5. Core area (ha), home range (ha), mean movement rate (m), and maximum distance moved (m) for northern bobwhites (*Colinus virginianus*) on the Encino Division of the King Ranch, South Texas, USA, in normal (Palmer Modified Drought Index [PMDI] = –1.99–1.99) and moist (PMDI >2.0) seasons during 2000–2006. We did not include data from normal winters in our statistical tests because of the small sample size. Asterisk (*) denotes significant differences across seasons and PMDI categories, $\alpha = 0.05$. Error bars are standard error.

DeVos and Mueller (1993) determined that northern bobwhite at Tall Timbers Research Station had larger home ranges in the summer of 1985 (19.8 ha ± 2.18 SD) than in 1986 (12.3 ha, SD = 1.39; $T = 2.91$, $P < 0.01$). The beginning of summer 1985 was dry but a moist winter followed by a normal early summer in 1986 may have promoted vegetation growth. West et al. (2012) found that northern bobwhite home ranges in Kentucky were larger in 2009 ($\bar{x} = 61.0$ ha, SE = 10.4 ha) than in 2010 ($\bar{x} = 44.9$ ha, SE = 5.9 ha), which was a wetter year. Movements may also change with precipitation; summer movements for northern bobwhite in southwestern Ohio were significantly longer (4.13 ± 1.00 km) in one dry year (2010) compared with a wet year (2011, 2.66 ± 0.52 km; Liberati and Gates 2012).

In addition to precipitation, temperature has an important effect on northern bobwhites in South Texas (Tri et al. 2012). Northern bobwhite broods in Oklahoma moved greater distances when temperatures were lower, and moved shorter distances in midday and afternoon when temperatures were higher (Carroll et al. 2015). Tanner et al. (2016) found that usable space for northern bobwhites decreased when temperatures rose above 35° C.

Weather and Plant Community Effects

As expected, northern bobwhites occupied all 3 plant communities in normal years as birds moved from feeding to loafing cover. We expected that in dry years birds would use mesquite shrubland because northern bobwhites choose loafing cover with greater canopies on hotter days (Guthery et al. 2000). In dry years birds used salty prairie and sandy mesquite savanna but not deep sand grasslands. The mean movement rate was shorter in dry years and similar in normal and moist years.

Northern bobwhites use a variety of habitats in different stages of succession (Stoddard 1931, Rosene 1969, Lehmann 1984). Brooding, nesting, and roosting northern bobwhites selected sites with more cover in Kansas (Taylor et al. 1999). Pasture land with woody brush cover dominates the South Texas landscape. Woody brush cover has been shown to be a critical part of northern bobwhite habitat (Kopp et al. 1998, Janke and Gates 2013, DeMaso et al. 2014). Janke and Gates (2013) found that while woody cover accounted for 11–17% available habitat, it surrounded 49% of the covey locations in Ohio. Long-term simulations of northern bobwhite indicated that populations were 2–3 times larger

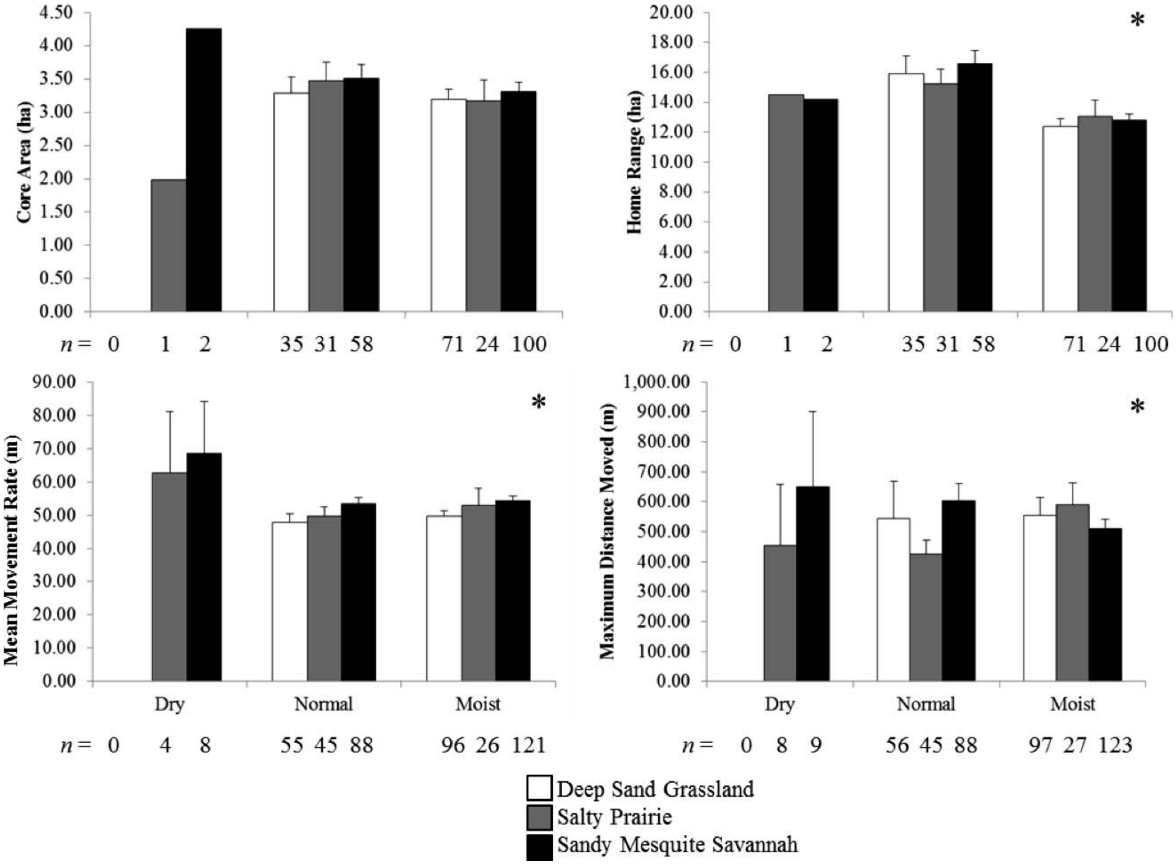

Fig. 6. Core area (ha), home range (ha), mean movement rate (m), and maximum distance moved (m) for northern bobwhites (*Colinus virginianus*) on the Encino Division of the King Ranch, South Texas, USA, in dry (Palmer Modified Drought Index [PMDI] <-2.0), normal (PMDI $= -1.99$–1.99), and moist (PMDI >2.0) years during 2000–2006. We did not include data from drought years in our statistical tests because of the small sample size. Asterisk (*) denotes significant differences across PMDI categories and plant community types, $\alpha = 0.05$. Error bars are standard error.

in pastures with 11–32% woody cover compared with a pasture with 5% woody cover (DeMaso et al. 2014). The quality of woody cover available to northern bobwhites is important as well (Lee 1994, Fies et al. 2002) and may affect northern bobwhite home range and movements. Lee (1994) described studies in Louisiana pineland and Mississippi where northern bobwhites had large home ranges (58.4 ha and 282 ha, respectively). Lee (1994) attributed these large home ranges to a need to search farther for food and to habitat degradation. Additionally, Fies et al. (2002) found that birds moved longer distances in more fragmented habitats. Grassland and woody cover in Encino was more contiguous in the landscape and was managed as northern bobwhite habitat.

It is clear from this and previous studies that northern bobwhite individuals occasionally move long distances. At Encino, most movements were less than what might be expected from genetic information (Wehland 2006, Eo et al. 2010, Miller 2014, Williford et al. 2014). Short-distance movements as documented in this study may be adequate to facilitate gene flow to nearby ranches but do not explain the lack of genetic differentiation seen at a larger scale (for example, from South Texas to the Great Plains, $F_{ST} = 0.023$; Miller 2014). Given the longer movements made by some northern bobwhites, it is worth considering that some birds move far enough to reach nearby ranches and that a few birds might make long-distance movements, facilitating gene flow.

MANAGEMENT IMPLICATIONS

Northern bobwhite home ranges and movements were small ($<$18 ha, $<$1 km), supporting previous assumptions that most northern bobwhites have small home ranges and short-distance movements. Northern bobwhites in this study chose plant communities that provided a variety of foraging areas, loafing cover, and nesting substrate. Providing a heterogeneous landscape of bare ground, herbaceous vegetation, and woody cover is important to management and conservation of northern bobwhite habitat.

Despite small home ranges and short movements, a small percentage (6%) of northern bobwhites made relatively long movements ($>$1.6 km). The potential gene flow resulting from such long-distance movements may be one of several factors driving the weak genetic structure of northern bobwhite populations in South Texas. Critical habitat is important to northern bobwhites that must adapt to changing conditions, while corridors that facilitate long-distance movements and dispersal are important to maintain gene flow and sustain local populations because abundance varies with annual weather conditions. For these few long-distance movements made by northern bobwhites, it is critical that there is contiguous habitat or corridors to allow for movement among populations.

SUPPLEMENTARY INFORMATION

Reference S1. Literature cited in Tables S1 and S2, a literature review of northern bobwhite (*Colinus virginianus*) movements and home ranges.

Table S1. Distance travelled for northern bobwhites (*Colinus virginianus*) in the United States, 1925–1975. Here, Recap. refers to the number of banded bobwhites that were recaptured or recovered during the study. Boldface: largest distance documented in the literature.

Table S2. Home range summaries for northern bobwhite (*Colinus virginianus*) in the United States, 1925–1975. Home ranges for coveys, rather than individuals, denoted with ^{c}.

Table S3. Northern bobwhites (*Colinus virginianus*) that moved more than 1000 m between observations from 2000–2006 on the Encino Division, King Ranch, Texas. Core Area (50% kernel, ha) and home range (ha) over the course of the study are provided. Date refers to date of movement (maximum distance moved, m). Age: HY (hatch year; juvenile), SY (second year), TY (third year), and A (adult).

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NORTHERN BOBWHITE NEST SITE SELECTION IN FIELD BORDERS

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ABSTRACT

Field borders are used to supplement early successional habitat critical for northern bobwhite (*Colinus virginianus*) nesting that is lost to modern intensive agricultural practices. The suitability of field border habitat for nesting may be affected by microhabitat characteristics at the site and patch scale and placement relative to various land-cover types at the landscape scale. We sought to determine whether bobwhite select nest locations at site, patch, and landscape scales. We collected microhabitat data (stem density, percent cover, and ground composition) and distance to land-cover type data (woody edge, crop, ditch, and road) from 26 bobwhite nests and 26 control sites in field borders in North Carolina, USA, during 2010 and 2011. We modeled nest site selection by comparing nests with random locations using conditional logistic regression at the site scale and logistic regression at the combined patch–landscape scale. We performed model selection using the small sample Akaike's Information Criterion (AIC_c). The top site-scale model showed that bobwhite selected for the presence of woody cover and avoided open soil at the nest. There was no clear top model at the combined patch–landscape level. In an agriculture-dominated landscape, managers should focus on microhabitat characteristics of field borders to improve suitability for bobwhite nesting.

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Key words: *Colinus virginianus,* field borders, nest selection, North Carolina, northern bobwhite

Northern bobwhite (*Colinus virginianus*) are associated with diverse, patchy landscapes predominated by large, open expanses and abundant woody edge (Rosene 1969, Roseberry and Klimstra 1984, Roseberry and Sudkamp 1998). Within these landscapes, bobwhite require microhabitats supported by the various stages of succession for survival and reproduction (Ellis et al. 1969). However, modern intensive agricultural practices adopted throughout much of the bobwhite's native range have reduced landscape heterogeneity (Warner et al. 2012). The precipitous decline of bobwhite populations over the past several decades (Sauer et al. 2014) can, in part, be attributed to this loss of early successional habitat (Guthery 1997, Hunter et al. 2001, Dimmick et al. 2002, Brennan and Kuvlesky 2005, Veech 2006).

Field borders—herbaceous buffers between cropland and adjacent cover types—may provide supplemental early successional habitat and increase bobwhite abundance in agricultural regions (Smith et al. 2005, Stamps et al. 2008, Doxon and Carroll 2010, Blank et al. 2011, Bowling et al. 2014). Summer and autumn bobwhite abundance was greater on farms in North Carolina, USA, after the establishment of field borders (Bromley et al. 2002, Palmer et al. 2005, Riddle et al. 2008, Bowling et al. 2014). Increases in the number of nesting attempts, improved nest success, or a combination of these 2 aspects of reproduction may be responsible for larger bobwhite populations on farms where field borders are present (Richardson 2016). More bobwhite nests were found on farms where field borders were implemented than on farms where field borders were not present with no difference in nest success between the 2 treatments (Puckett et al. 1995).

The suitability of field border habitat for bobwhite nesting is likely influenced by micro and macrohabitat variables operating simultaneously at multiple scales. Bobwhite avoid bare soil at the nest site throughout their range (Taylor et al. 1999, Townsend et al. 2001, Lusk et

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al. 2006, Rader et al. 2007). The vegetation at the nest is generally taller (Taylor et al. 1999, Arrendondo et al. 2007, Rader et al. 2007), denser and composed of more strata (Townsend et al. 2001, Arrendondo et al. 2007, Rader et al. 2007, Collins et al. 2009). Bobwhite seem to favor nesting locations that offer greater concealment than the preponderance of available habitat, but there is little evidence to support that the structure of vegetation differs between successful and unsuccessful nests (Townsend et al. 2001, Rader et al. 2007). Bobwhite have not been observed to exhibit selection for microhabitat variables at a patch scale in association with nesting (Taylor et al. 1999). No studies to date have focused on bobwhite nest placement in field borders relative to land-cover types. However, nest placement near field–forest ecotones, which are common in agricultural landscapes, has been shown to adversely impact success in other species (Gates and Gysel 1978).

None of the previous nest-site selection research was conducted in field borders habitat. Selective pressures that drive nest placement in field borders may differ from the larger, contiguous habitats of prior studies. Nest depredation risk and microclimate stressors are likely intensified in field borders habitat. Increased edge presence in field borders and potential use as travel corridors by predators, facilitated by the linear shape of the habitat and persistence in a disturbed landscape may collectively result in greater depredation risk than contiguous habitat (Shalaway 1985, Camp and Best 1994, Pedlar et al. 1997, Clark and Bogenschutz 1999, Dijak and Thompson 2000). The recruitment potential of field borders may be outweighed by increases in predator density if the habitat has utility for multiple species (Puckett et al. 1995). Microclimate characteristics of field borders may also influence nest placement. The planting or harvest of adjacent crops or accidental application of herbicide could induce thermal stress that would decrease the probability of nest success (Carroll et al. 2015). Bobwhite nesting decisions at multiple scales are likely reflective of both selective pressures.

A better understanding of the interaction between habitat placement within the landscape matrix, microhabitat composition at the patch and nest level, and the relationship of these variables to nest success is critical to continued recovery efforts for bobwhite (Duren et al. 2011). Knowledge of landscape-level effects is of great importance to the implementation of supplemental habitat (Riddle et al. 2008, Bowling et al. 2014) whereas awareness of favorable microhabitat characteristics is essential to field border maintenance (Greenfield et al. 2002). Field border management must be informed because of the significant investment of monetary and technical resources required to create and maintain this supplemental habitat.

Our study sought to model bobwhite nesting decisions in field border habitat at 3 spatial scales. Our objectives were to determine whether, 1) at the site level, microhabitat variables influenced nest placement relative to the immediately adjacent habitat, 2) at the patch level, microhabitat variables influenced utilization of field border for nesting, 3) at the landscape level, distance to various cover types influenced utilization of field border for nesting. We hypothesized that top models at the site and combined patch–landscape scale would include structural and compositional microhabitat parameters that contribute to greater concealment at the nest site. We also hypothesized that the most competitive patch–landscape scale model would demonstrate avoidance of woody edges.

STUDY AREA

We conducted our study on a 1,619-ha Murphy-Brown, LLC., agro-industrial hog farm located in Bladen County, North Carolina, a part of the southeastern Coastal Plain. Our study site consisted of approximately 72 ha of field borders maintained in an early successional shrub–grassland mixed state through a combination of disking, mowing, and selective herbicide application. All field borders were adjacent to a crop field on ≥ 1 edge. Crop land on the farm was cultivated rotationally on an annual basis between soybeans, corn, and winter wheat. We selected 141 linear and 24 nonlinear field borders for use in this study. Linear field borders separated or defined the periphery of the agricultural fields. Linear borders were approximately 0.41 ± 0.34 ha (mean ± SD) in size and varied in length (509.08 ± 305.25 m) and width (9.02 ± 6.40 m). Nonlinear field borders were irregularly shaped field corners. They averaged 0.80 ± 0.72 ha in size. The predominant vegetation in the field borders was marestail (*Conyza canadensis*), dog fennel (*Eupatorium capillifolium*), little bluestem (*Schizachyrium scoparium*), blackberry (*Rubus* spp.), salt myrtle (*Baccharis halimifolia*), and other herbaceous or grassy species. The species composition was the result of a mixture of plantings and natural germination after agricultural cessation. A few nonlinear field borders were composed of planted native warm season grasses, including big bluestem (*Andropogon gerardii*), little bluestem, and switchgrass (*Panicum virgatum*).

METHODS

Nest Searching

We searched field borders for bobwhite nests ≥ 2 times in 2010 and ≥ 4 times in 2011. During each search rotation, we selected field borders in a random order. However, field borders separated by a ditch were paired for searching to minimize disturbance to the adjoining border. We searched each field border systematically by walking parallel transects and carefully parting the vegetation with sticks to detect the presence of nests. Each observer searched an area equal to their arm length on both sides of the transect. We walked as many transects as was necessary to thoroughly search the entire field border. We intensified our search in areas where behavioral cues, such as bobwhite vocalizations and flushes, indicated likely nest presence. Nests encountered opportunistically while achieving other research objectives were also included in the study. We were alerted to the presence of one nest through behavioral indicators and encountered another opportunistically over the course of 2 field seasons.

Linear field borders separated by a ditch were searched by a pair of individuals each walking parallel transects on the same side of the channel in wide borders or opposite sides in narrow borders. The search strategy for nonlinear field borders was dependent on the border's overall geometry. Two individuals either started on opposite ends of the field border, walking parallel transects until converging in the center, or both individuals walked side by side canvasing the entirety of the area. If we found a nest, we marked the site approximately 3 m away with flagging tape and recorded the location with a handheld Global Positioning System (GPS) unit. We also marked vegetation that had the characteristic covered dome construct of a bobwhite nest, but only treated these sites as nests if we encountered an egg during the next observational period. We monitored nests periodically until a success, failure, or abandonment outcome could be determined, after which we measured vegetation characteristics and proximity to landscape-level features at each site (Westmoreland and Best 1985, Major 1990, Martin and Geupel 1993, Ralph et al. 1993). We took vegetation measurements within 1 week of observed nest failure with nest and control site measurements in the same field border typically performed on the same day.

Vegetation Sampling

We quantified vegetation characteristics at nest sites, as well as 2 associated random sites within 5–20 m of the nest center to model site-scale selection. We considered a nest site or associated site to include all habitat within a 1-m radius of a central point of interest. We chose associated sites using a random number generator to select an azimuth and random distance between 5 and 20 m from the nest. We took measurements immediately inside the field border edge at the respective azimuth if an associated site fell within an adjacent cover type.

We also randomly selected a control site from the field borders included in our search rotation to model patch selection. We considered a single field border to be synonymous with a patch. Coincidentally, there was no overlap between the field borders that contained control sites and nests within a field season. Between field seasons, there was only a single case where a field border selected as a control in 2010 was found to contain a nest during the subsequent field season. Field borders containing control sites were typically searched both before and after measurements were taken in accordance with the scheduled rotation, providing reasonable certainty of nest absence. Therefore, control sites should be considered representative of field borders where quail did not nest during a respective field season. Similar to the nest site, we measured the attributes of the vegetation at the control site as well as 2 associated sites within 5–20 m of the initial location. We averaged the measures of the control site and associated sites to produce a general characterization of field border habitat.

We selected the control site by first randomly choosing a field border and then arbitrarily designating a location within that field border constrained by border dimensions. We selected the location of the control site in linear field borders using 2 randomly generated distances corresponding to the length and width, but not exceeding the maximum length and width of the field border. Starting from the primary point of access for the field border, we walked the length-associated distance down the crop edge, then entered the width-associated distance into the border and took vegetation measurements at this point. In nonlinear field borders, we treated the edge adjacent to the crop field as the border's length. We walked a random distance along this edge beginning at the terminus closest to our point of searching access. We defined the width of the border as the maximum length of a perpendicular transect drawn from this point to the opposite side of the border.

At all nests, control sites, and associated sites we assessed ground composition (i.e., woody plants, grass, open soil, leaf litter, and herbaceous), percent cover (an estimate of visual obscurity of the nest), and stem density of woody plants. We recorded ground composition using a 1-m × 1-m quadrat centered on the point of interest. We classified elements within the square frame as woody plants, grass, open soil, leaf litter, or herbaceous vegetation, and described the composition using 5% intervals with the total for all coverage classes summing to 100%. We characterized percent cover and stem density using a Robel pole with 15 0.1-m sections centered on the site of interest (Robel et al. 1970). An observer standing approximately 3 m from the pole estimated percent cover per section at 5% intervals, adjusting position accordingly to ensure readings were taken at eye-level. We also quantified the density of woody stems by counting the number of woody stems touching each of the 15 sections of the Robel pole. We measured both percent cover and stem density at 3 separate random azimuths and averaged percent cover across the azimuths and 15 sections of the Robel pole to produce a single value for the site.

Edge Sampling

We measured the distance to land-cover types (woody edge, crop, ditch, and road) from the center of both nest and control sites. We assessed distance to crop and ditch with a tape measure stretched from the site of interest to its intersection with the nearest edge of the cover type. We could not determine the proximity of nest and control sites to the closest woody edge or road with the same measurement technique because of the scale of our study area. Instead, we ascertained the distance to nearest woody edge, defined as the edge of a forest or hedge row with trees, using a range finder held over the center of the nest or control site. We used the measuring tool in ArcGIS (Version 9.3; ESRI, Redlands, CA, USA) and satellite imagery to determine the distance to the closest road. We also used this technique to determine distance to woody edge if obstructions in our line of site prohibited use of a range finder.

Table 1. Akaike's Information Criterion corrected for small sample size (AIC_c) and weight (w_i) for site scale models of differences in vegetation variables between northern bobwhite nests and associated random sites in field borders, North Carolina, USA, 2010–2011.

Model description	K	AIC_c	ΔAIC_c	w_i
Woody + open soil	3	40.852	0.000	0.527
Global	6	42.857	2.005	0.193
Open soil	2	44.113	3.261	0.103
Open soil + herbaceous	3	44.155	3.303	0.101
Open soil + grass	3	45.389	4.537	0.055
Woody	3	47.718	6.866	0.017
Woody + herbaceous	2	51.550	10.698	0.003
Grass	3	53.604	12.752	0.001
% cover	2	59.747	18.895	0.000
Herbaceous	2	60.461	19.609	0.000
Grass + herbaceous	2	60.590	19.738	0.000

Statistical Analysis

To model nest site selection at the site level, we used conditional logistic regression to compare variables measured at the actual nest site to the 2 associated random sites. To model nest site selection at a combined patch–landscape level, we used logistic regression to compare variables measured at the nest sites with the averages of the control sites and 2 associated sites. We performed model selection using the small-sample Akaike's Information Criterion (AIC_c). In each case the tested models included a global model, all single-variable models, and all 2-variable combinations of cover types. We excluded stem density as a parameter because of a high degree of multicollinearity with woody vegetation. Sum constraints also resulted in a lack of independence among the quadrat data response variables so we chose to eliminate leaf litter from the final analyses because we perceived it to be the cover type with the least biological relevance for our study location.

RESULTS

We located 26 bobwhite nests during the 2010 and 2011 field seasons. We also assessed an additional 26 control sites within field borders that did not contain nests during the respective field season. The top site-scale model included open soil and woody parameters (Table 1). Beta values indicate that bobwhite selected against open soil at the nest site ($\beta = -0.2233$, SE = 0.0865), but favored a greater presence of woody vegetation ($\beta = 0.0507$, SE = 0.0250). Open soil was present in the top 5 models and appears to be the strongest predictor of nest placement (Relative Importance Value = 0.979; Table 1). The next 2 models included woody cover as a parameter, indicating its secondary significance as a predictor of habitat suitability for nesting (Relative Importance Value = 0.740; Table 1). Open soil was also the strongest single variable model behind the top and global models, followed by woody cover (Table 1). Nests had a median of 5% open soil and a range (R) of 25% compared with 10% open soil (R = 47.5%) at associated sites (Table 2). The distribution of the open soil variable at the nest site was strongly left-skewed with an absence of open soil from 8 of the nest locations. Nests had a median of 0% woody cover (R = 80%) compared with 1.25% at random sites (R = 55%), which initially seems to contradict the trend of the model betas (Table 2). However, like open soil, the distribution of the woody cover variable was strongly left-skewed with 14 of the 26 nests we encountered having no woody vegetation. The maximum percentage of woody cover observed at an adjacent subplot was 55%, while 4 nests had >60% woody cover. There was model uncertainty at the combined patch–landscape level (Table 3).

Table 2. Median (M), range (R) for ground cover, percent cover and stem density (%) of northern bobwhite nests and the average of adjacent random sites in field borders, North Carolina, USA, 2010–2011.

	Nest		Adjacent site	
Ground cover	M	R	M	R
Woody plants	0.0	80	1.25	55.0
Grass	22.5	75	12.50	72.5
Open soil	5.0	25	10.00	47.5
Herbaceous	25.0	70	26.25	50.0
Percent cover	48.39	55.89	46.39	54.39

DISCUSSION

Bobwhite nest placement within field border habitat was influenced solely by microhabitat characteristics at the site level. Bobwhite selected nesting locations with less open soil and more woody cover than adjacent

Table 3. Akaike's Information Criterion corrected for small sample size (AIC_c) and weight (w_i) for combined patch–landscape models of differences in vegetation variables and distance to land-cover types between northern bobwhite nests and random control sites in field borders, North Carolina, USA, 2010–2011.

Model description	K	AIC_c	ΔAIC_c	w_i
Open soil + herbaceous	3	69.446	0.000	0.206
Woody + grass	3	69.467	0.021	0.204
Grass + open soil	3	70.762	1.316	0.107
Open soil	2	71.331	1.885	0.080
Global	10	71.417	1.970	0.077
Herbaceous	2	72.124	2.678	0.054
Woody + open soil	3	72.493	3.047	0.045
Grass	2	72.647	3.201	0.042
Grass + herbaceous	3	72.828	3.382	0.038
Woody + herbaceous	3	73.762	4.316	0.024
Road	2	73.990	4.544	0.021
Woody edge	2	74.066	4.620	0.021
Distance	5	74.169	4.723	0.019
Vegetation	6	74.337	4.891	0.018
Ditch	2	74.554	5.108	0.016
Crop	2	75.217	5.771	0.012
Woody	2	76.039	6.593	0.008
% cover	2	76.072	6.626	0.008

habitat. Bobwhite in our study may have avoided nests with abundant open soil because these sites did not provide adequate concealment from predators. Conversely, bobwhite may have selected for nesting locations with a greater presence of woody vegetation because increased concealment reduced depredation risk. Overall concealment at the nest site, represented by the percent cover parameter in our model set, was a poor predictor of site selection in our study. This may indicate that the cover types bobwhite favored or avoided may have specific structural characteristics or use values that are of greater importance than the total amount of vegetation.

Avoidance of open soil at the nest is the only ground cover attribute that is consistently important throughout the bobwhite's range. Taylor et al. (1999), Townsend et al. (2001), Lusk et al. (2006), and Rader et al. (2007) observed bobwhite selection against bare ground at the nest site in contiguous grassland, rangeland, and Conservation Reserve Program (CRP) field habitats. Each of these studies attributed the avoidance of open soil to selection for greater concealment at the nest site. However, the presence of open soil at the nest site may have a differential impact on survival throughout the bobwhite's range. Townsend et al. (2001) found that bobwhite nests with less open soil had a greater probability of success; whereas Lusk et al. (2006) observed that although bobwhite selected for less open soil at the nest, bare ground exposure was positively correlated with nest success. Lusk et al. (2006) attributed their findings to human alteration of bobwhite habitat on rangelands that may have uncoupled selection criteria from the anticipated benefit of greater nest success. We assumed that bobwhite avoidance of open soil at nests in field borders was driven by increased survival probability, but selection criteria may also be divorced from success at our field site because field borders are highly disturbed, man-made habitats. Further exploration of the relationship between ground cover classes and nest success in field border habitat is necessary to determine whether selective pressures have become uncoupled from nest success.

Structural characteristics of vegetation at the nest that increase concealment may be of greater importance to bobwhite than specific cover types. We attributed bobwhite selection for the presence of greater woody vegetation at the nest to increased concealment. However, bobwhite selection for microhabitat characteristics must be driven by a secondary factor other than total concealment because percent cover at the nest was comparable to random sites. Bobwhite may have selected for structural attributes of woody species including height, distribution of cover, or concealment of the nest from an aerial perspective. While different cover types may serve a similar function across the bobwhite's range, it is possible that woody species most adequately fill this role in our study area. Functional tradeoffs of vegetation would also explain the absence of woody vegetation from over half of our nest sites and secondary importance in our model set. Woody cover may have desirable structural attributes for nesting but vegetation with similar structural qualities may serve as an adequate substitute if woody cover is not available. No similar tradeoffs exist for open soil, which may explain why it was the strongest predictive parameter. We did not measure structural characteristics directly and those that could be derived from Robel pole data were masked by averaging the data for site comparisons.

Woody cover was only found to be a predictor of nest site selection in a narrow portion of the bobwhite's range in northern Texas and Oklahoma until our findings (Townsend et al. 2001, Lusk et al. 2006). Other authors attributed the relationship between the Townsend and Lusk studies to the value of a particular woody species because the vegetation composition of both study locations was similar (Rader et al. 2007). Although our study site is found at a similar latitude, the plant community in our field border habitat had very little overlap with these previous studies, contradicting the species value hypothesis. Regional similarities in the predator community may have resulted in similar patterns of cover type selection. Factors unrelated to nest predation but reliant on nest vegetation structure, such as nest microclimate, also would be subject to similar selective pressures and may be tied to climatological similarities at comparable latitudes. Any similarities between these two disparate regions of the bobwhite's range are merely speculative and further research is needed to determine whether there is any relationship between the importance of woody vegetation at nest sites in both areas.

Microhabitat characteristics that influenced nesting decisions within a field border did not determine which field borders bobwhite utilized for nesting, defined for the purposes of our study as patch selection. Model uncertainty at the patch scale was likely representative of the homogeneity of vegetation in all borders included in our study. Similar ground composition between borders did not predicate patch selection because all habitat was equally suitable for nesting. Our results were comparable to Taylor et al. (1999), who noted the absence of patch selection on contiguous rangelands.

Bobwhite utilization of field borders for nesting was also not influenced by distance to land-cover types, defined as landscape scale selection. Piispanen and Riddle (2012) were unable to show that nest placement relative to land-cover types conferred any nest survival advantage. Therefore, nest placement with respect to land-cover types may not have been observed because it does not contribute to reproductive fitness at our study site.

Although model uncertainty at the combined patch–landscape scale indicated that microhabitat variables and distance to land-cover types were similar between all field borders in our study, bobwhite did not utilize all borders for nesting. Nonuse is likely a consequence of some variable our study failed to capture. Bobwhite may have avoided some field borders because they were unsuitable for nesting. For example, bobwhite would likely not have nested in habitat supporting a large population of predators. Field borders may have been suitable for nesting but dispersal to the habitat was restricted by some feature of the agricultural landscape. There also may not have been a great enough abundance of bobwhite at our study site to utilize all of the habitat suitable for nesting. We found 9 nests during the 2010 field season and 17

Table 4. Mean distance to landscape features (m) of northern bobwhite nests and control sites in field borders, North Carolina, USA, 2010–2011.

	Nest		Control site	
Feature	$\bar{x}$	SE	$\bar{x}$	SE
Woody edge	401.77	53.60	296.64	47.66
Crop	4.93	0.92	3.72	0.81
Ditch	8.35	2.98	4.53	0.97
Road	169.25	27.91	249.46	47.35

nests during the subsequent summer. This dramatic increase in nest initiations may indicate underutilization of habitat resources available for nesting. However, further research is needed to determine why bobwhite are not utilizing all seemingly suitable field borders for nesting.

Negative edge effects resulting from proximity to woody cover types observed in other species may not have influenced nest placement on our study site because of broader landscape context (Gates and Gysel 1978, Andren and Anglestam 1988, Marini et al. 1995, Woodward et al. 2001, Sperry et al. 2009). The average nest in our study was approximately 400 m from the nearest woody edge (Table 4). Weatherhead et al. (2010) did not observe edge effects for nesting birds in a field environment within 74 m of a woody edge, <25% of the distance observed in our study. The average control location in our study was nearly 300 m from the closest woody edge, indicating that all available nesting habitat may be sufficiently far from woody edges in an agriculture-dominated landscape to avoid the increased predation risk associated with woody edges. Piispanen and Riddle (2012) did not observe any bobwhite nests in field borders on farms in a forest-dominated landscape. This observation supports the findings of Duren et al. (2011), which noted that bobwhite select against both highly fragmented early successional habitat and agricultural lands juxtaposed with forest edge. Although field borders may have less influence on bobwhite occupancy rates than landscape composition (Bowling et al. 2014), the nesting habitat they provide may contribute to increases in local abundance. Within a suitable landscape, field borders placement may be flexible and prove to be a valuable conservation tool to maximize bobwhite abundance.

MANAGEMENT IMPLICATIONS

Field-border management practices should encourage some presence of woody vegetation and minimize the amount of open soil. Within an agricultural landscape, field border placement may be flexible. The construction of additional field-border habitat does not appear to be constrained by proximity to various land-cover types. However, the relationship between our study variables and nest success may warrant further investigation to determine whether selective pressures have become uncoupled in field border habitat.

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BREEDING SEASON SURVIVAL AND NESTING OF NORTHERN BOBWHITE ON NATIVE PRAIRIE VERSUS TRADITIONALLY MANAGED CONSERVATION AREAS IN SOUTHWESTERN MISSOURI

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) management on Missouri Conservation Area lands has traditionally focused on providing an interspersion of grass, crop, old field and woody cover to enhance edge habitat often juxtaposed with disked idle areas and food plots. This traditional approach, or the Intensive Management Model (IMM), is often implemented with the goal of providing all essential habitat components within a 40-acre area. While this model can produce useable quail habitat in agriculture-dominated landscapes it may not be the most effective or efficient approach to producing quail in grassland-dominated landscapes found in southwest Missouri. Conservation area mangers for the Missouri Department of Conservation (MDC) have historically implemented IMM in these grass-dominated landscapes; however in a few areas managers have begun using historical ecological processes, such as fire with grazing, or the Extensive Management Model (EMM) in conjunction with IMM or as the primary means for producing the patchy habitat mosaic preferred by bobwhite quail. In 2015, MDC began a 5 year study radio marking 60 individuals per area on 4 areas (2 IMM and 2 EMM) to compare the utility of these two models and the habitat conditions they create on breeding season vital rates (survival and production). Over the first 2 years of this study, EMM areas had higher breeding season survival (0.414 compared to 0.275) and nesting success (0.437 compared to 0.355) relative to IMM areas. Additionally, covey break-up and nest initiation were in general earlier, and clutch sizes were larger on areas managed with EMM than on areas managed with IMM.

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Key words: breeding season, *Colinus virginianus*, grazing, northern bobwhite, Missouri, reproduction, survival

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EVALUATING TWO TRAP-AND-RELEASE METHODS FOR BOBWHITES

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ABSTRACT

Numerous methods exist for capturing northern bobwhite (*Colinus virginianus*) including various net configurations and baited, wire-funnel traps. The latter represents the most commonly used technique whereby more than 97% of the studies in the current body of literature report using Stoddard's (1931) standard quail trap for capturing bobwhites. Some researchers, however, employed multiple methods of capture for the same study. Regardless of the technique used, birds are either worked up directly in the field or held overnight and released the next day. Each of these approaches has their distinct advantages and limitations, and may vary with respect to their overall impact on bobwhite behavior and survival germane to stress incurred during capture, handling, and/or transport. Despite the inherent difference in capture and handling time, no known studies have evaluated the influence of these two capture methods on bobwhites. Yet, the tenability of the information gained from research is predicated on the notion that our methods do not influence the individuals being studied. During 2014 – 2015, we captured bobwhites ($n = 664$) on Tall Timbers Research Station (TTRS, ~1570 ha) using standard funnel traps during fall (Oct/Nov), winter (January) and spring (Mar/April). All birds were leg-banded and one subset (Cohort 1;$n = 108$) was radio-tagged, worked up in the field and release immediately at the capture site and a second subset (Cohort 2;$n = 212$) was transferred to holding boxes, held overnight and the next morning they were radio-tagged and released nearby the capture site. I evaluated daily survival rate for each of the 4 groups (radio-tagged cohorts, banded-only controls) using Burnham's joint model in program MARK. Preliminary results indicate the daily survival for cohort 2 was moderately better than cohort 1 but similar to control groups. Additional data will be incorporated upon the completion of March 2016 trapping season.

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Key words: *Colinus virginianus,* capture, handling effect, mark-recapture, northern bobwhite*,* wire trap

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ESTIMATES OF NORTHERN BOBWHITE NEONATE SURVIVAL

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ABSTRACT

Neonate survival is an important but poorly understood component of northern bobwhite (*Colinus virginianus*) population dynamics. We used a combination of thermal imagery (forward-looking infrared [FLIR]) and radio-telemetry to estimate survival from time of hatch to fall recruitment. During 2013 – 2015, we tracked bobwhites and captured broods at $\sim$11 days of age using the corral technique. In addition to patagial tagging each neonate captured, we sutured radio-tags (0.76 g) on a subset of neonates ($n = 56$), and located them 3-4 times daily using radio-telemetry to determine fate and cause of mortality. We modified the Dail-Madsen model in a Bayesian framework to estimate survival, while accounting for brood amalgamation, from data collected with FLIR and the known-fates to estimate survival of radio-tagged birds. We observed a curvilinear relationship (= 0.047, SE = 0.014) between age and survival such that daily survival rates gradually increased up to 10 weeks of age at which time survival reached an asymptote. The average daily survival rate for bobwhite neonates during the first 2 weeks of age was 0.9278 (95% CrI = 0.5908 – 0.9987), 0.9814 (SE = 0.0049) for weeks 3 to 10, and 0.9979 (SE = 0.0017) after 10 weeks of age. Linking daily survival estimates from FLIR (0-11 days) with radio-tagged ($\geq$12-days) survival, we surmise that only small portion ($\sim$18.5%) of chicks hatching during the peak nesting period (June-July) survive to fall recruitment. Despite the lack of information on neonate survival, to date, numerous population models incorporate estimates of chick survival at 45-50% to fall recruitment. However, our results suggest that those estimates are high and may report spurious results. We further suspect that hatch timing (June vs Sep) and weather likely influence daily survival rates of neonates and may substantially impact overall fall recruitment.

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Key words: *Colinus virginianus*, chick, FLIR neonate, northern bobwhite, survival, suture, thermal imagery

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PATCH SIZE AND NEST DENSITY INFLUENCE NEST SURVIVAL

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ABSTRACT

Nest predation is the primary cause of avian nest failure and therefore an important driver of avian population growth. Studies indicate that landscape context plays an important role in nest success, and although this is widely attributed to changes in nest predator communities, landscape context also influences nest density which affects predator search area and effort. Much debate remains as to whether specifically the size of a habitat patch or the density of nests has the greatest effect on nest predation rates. We explored the interactions between landscape context, predator efficiency, and nest survival. Northern bobwhite quail (*Colinus virginianus*) possess specific habitat requirements within a small home range and are a short-lived species that relies upon high reproductive performance, which make them the ideal system to test the extent to which landscape context affects nest predation rates. We investigated the extent to which the size of a grassland patch versus nest density affects nest survival by studying the predation rates of 617 artificial nests during two 23 day trials on 12 study sites in south central Nebraska. To examine the effects of patch size, we selected 6 study sites that were small patches of grassland (including pastures and Conservation Reserve Program fields) ranging in size from 40-60 ha and 6 study sites that were approximately 50 ha sections of larger contiguous grasslands. A high density of artificial nests were placed on half of the small and large patch study sites with the remaining sites having a low density of nests, for the second trial the nest density treatments were switched for each site.

Citation: Simonsen, V. and J. J. Fontaine. 2017. Patch size and nest density influence nest survivaL. National Quail Symposium Proceedings 8:235.

Key words: *Colinus virginianus*, nest survival, landscape context, northern bobwhite, and predation

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EFFECTS OF GROWING SEASON FIRE ON NORTHERN BOBWHITE NEST SITE SELECTION AND SURVIVAL

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ABSTRACT

Restoration and management of longleaf pine (*Pinus palustris*) communities necessitates frequent prescribed fire. Prior to human colonization of the southeastern United States thousands of years ago, longleaf pine forests burned primarily during the growing-season as a result of lightning-ignited fires. Growing-season prescribed fire may suppress woody vegetation and promote herbaceous groundcover better than dormant-season fire. Despite the potential ecological benefits of growing-season fire, many land managers use only dormant-season prescribed fire to avoid destruction of ground nests, including those from northern bobwhite (*Colinus virginianus*). Our objective was to determine bobwhite nest survival and nest-site selection in the presence of early, growing-season prescribed fire on a 3-year return interval. We compared vegetation composition and structure at nest sites and paired random sites to identify important predictors of nest-site selection and to evaluate the effects of habitat covariates on nest survival. We captured bobwhite and attached radio transmitters. Radio-marked individuals were tracked to locate nests and determine nest survival. We documented 2 nests that burned during a growing-season prescribed fire. All 14 nests were located within units that were burned at least 2 years prior, putting these nests at a greater risk for being destroyed by prescribed fire that occurred on a 3-year return interval. We suggest that restricting early, growing-season prescribed burning to April through early June should limit an overlap between prescribed burns and the peak of northern bobwhite nesting season, which occurred mid-July at our study site. Additionally, longer fire return intervals may be needed to allow development of woody understory structure selected by bobwhites for nesting, especially on poor soils like those on our study site in the Sandhills physiographic region.

Citation: Rosche, S. B., C. E. Moorman, C. S. Deperno, and J. G. Jones. 2017. Effects of growing season fire on northern bobwhite nest site selection and survival. National Quail Symposium Proceedings 8:236.

Key words: growing season prescribed fire, *Colinus virginianus,* northern bobwhite, North Carolina, Fort Bragg Military Installation, longleaf pine, nest survival, nest-site selection, fire frequency

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INFLUENCE OF NORTHERN BOBWHITE NEST SITE SELECTION ON NEST SURVIVAL IN AN AGRICULTURAL LANDSCAPE

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ABSTRACT

Working farms provide excellent potential for conserving northern bobwhite (*Colinus virginianus*) habitat in agricultural landscapes. Managing for areas of early successional vegetation can increase bobwhite abundance with little reduction in crop production on working farms, but the mechanisms behind the increase is not well known. Our objective was to determine nest site characteristics that may predict nest initiation and survival on agricultural lands to inform future management activities. We radio-collared 241 wild bobwhite on 1 farm with and 2 farms without bobwhite habitat management in southeastern North Carolina. Study sites consisted of a 1,740-ha farm with 9% of property actively managed for early successional cover using areas planted in native vegetation and fallow field borders, a 170-ha farm with 2% of property in early-successional field borders monitored in 2014, and a 395-ha farm with no previous early successional management efforts monitored in 2015. We monitored nests ($n = 71$) from 15 May to 30 September, 2014 and 2015. We compared vegetation cover between nests and paired reference sites within 250 m of each nest using a generalized linear mixed-effect model. We used measurements of vegetation cover types at nest sites as predictors of nest survival using the Program MARK nest survival model. Bobwhite on the farm with habitat management exhibited higher nest initiation (1 nest/2 marked individuals) than those on unmanaged farms (1 nest/4 marked individuals). On the managed farm, 76% of nests were located in fallow early successional vegetation. Percent forb cover ($P = < 0.001$) was greater at nest sites on managed ($\mu = 53.61$, $SE = 4.32$) than unmanaged ($\mu = 17.01$, $SE = 2.49$) farms. Bobwhite selected nest sites with greater forb cover ($\beta = 1.08$, $SE = 0.21$) than reference sites. Daily nest survival was 0.962 ($SE = 0.007$) with no covariates that described variation in nest survival rates. Results indicate increasing fallow forb cover on agricultural lands can benefit nest initiation rates by increasing the cover bobwhite select for nesting.

Citation: Richardson, A.D., C. E. Moorman, C. A. Harper, M. D. Jones and B. M. Strope. 2017. Influence of northern bobwhite nest site selection on nest survival in an agricultural landscape. National Quail Symposium Proceedings 8:237.

Key words: northern bobwhite, *Colinus virginianus*, nest survival, agriculture, private land management, field border

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TRIPLE BROOD PRODUCTION BY NORTHERN BOBWHITES

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ABSTRACT

Most aspects of northern bobwhite (*Colinus virginianus)* life history are well understood and well documented, including their ability to "double brood" (defined as the same hen successfully hatching 2 broods during a single nesting season). Less understood are the ability and/or prevalence of "triple broods" in the life history of bobwhites. Occasional citing in the literature of triple brooding is often unclear as to whether reference is being made to the attempt at hatching 3 broods in a season or actually doing so. This confusion stems from the interchanging use of the words brood and clutch. While Webster defines "clutch" as either 1) a nest of eggs, or 2) a brood of chicks; "brood" is clearly defined as a group of birds hatching at one time. A closer look at the referenced studies reveals incidences of "triple clutching" where a single hen incubated three nests in one summer, but no published record of a true triple brood. The strict definition of triple brood should be: the same hen successfully hatching 3 broods in a single nesting season. Our nest data from radio-tagged birds collected in the Albany, GA area suggest that this phenomenon is extremely rare. From 1992-2016 we radio-tagged and monitored 2,607 hens during the nesting season on our primary study area in Baker County, GA. These birds produced 1,463 incubated nests and hatched 768 broods. Double broods were fairly common (n = 91) and occurred in all but two of the 25 nesting seasons. Only one incidence of true triple brooding has been documented on this study area during this time period. Adult mortality, nest loss, and the limited duration of the nesting season all work against this level of production. While an interesting aspect of the bird's natural history, the extremely low rate of occurrence makes it insignificant from a population standpoint.

Citation: Sisson, D. C. 2017. Triple brood production by northern bobwhites. National Quail Symposium Proceedings 8:238.

Key words: *Colinus virginianus,* double broods, Georgia, northern bobwhite*,* triple broods

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AN ANALYSIS OF THE INTERACTIONS BETWEEN WEATHER AND LAND USE ON MIDWESTERN GAMEBIRD POPULATIONS USING HISTORICAL DATA—A PRELIMINARY REPORT

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ABSTRACT

Concern surrounding species' abilities to cope with a changing climate and variable land use presents opportunities to look forward toward solutions while investigating historical trends to assess the interaction of land use and weather. Uncertainty surrounding population responses to increased severity and frequency of severe weather associated with climate change presents challenges for making informed management decisions for a suite of already declining bird populations, including huntable populations of socially and economically important game birds, such as northern bobwhite (*Colinus virginianus*). Historical data are a rich resource for developing *a priori* hypotheses and models predicting species' responses to climate change and continued variation in land use. We are utilizing 30 years of historical data to model the responses of northern, ring-necked pheasant (*Phasianus colchicus*), and wild turkey (*Meleagris gallopavo*) to land use change and weather within a gradient of land use and climate in Nebraska, Kansas, Iowa, and Missouri. Mixed models incorporating agricultural acreages, relative abundances of gallinaceous birds from the annual Breeding Bird Survey, and historical precipitation and temperature data built at the county-level will illuminate broad scale trends and enable us to draw conclusions about future population responses. We are finding expected differences in population trends between states within a climatic gradient, and varied responses to temperature and precipitation among gallinaceous species, where different annual periods are more or less crucial for different species despite similar life history characteristics. We expect that further modeling will continue to elucidate critical thresholds for birds in the Great Plains in terms of weather and habitat, allowing us to make strong recommendations to managers preparing to deal with the implications of climate change.

Citation: Lipinski, A. R. and J. J. Fontaine. 2017. An analysis of the interactions between weather and land use on midwestern gamebird populations using historical data– a preliminary report. National Quail Symposium Proceedings 8:239.

Key words: *Colinus virginianus,* northern bobwhite, climate change, severe weather, land use, population trends, mixed modeling, Great Plains ecology, Program R

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EVALUATION OF LAND RESTORATION PRACTICES ON NORTHERN BOBWHITE PRODUCTIVITY IN NORTH-CENTRAL TEXAS—PRELIMINARY RESULTS

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ABSTRACT

The decades long decline in grassland avian populations is ultimately attributed to changing land use throughout the United States. Due to their economic importance and status as a healthy grassland indicator species, attention focused towards land management for northern bobwhite (*Colinus virginianus*) benefits other grassland vertebrate and invertebrate species. Land restoration practices offer opportunities to mitigate the declines in northern bobwhite populations. While several studies focus on restoring land for northern bobwhite, this study addressed the effectiveness of such restoration practices. We radio-marked female bobwhite from April to July 2016 and located the birds every three to five days to gather land use information at female diurnal locations. We also placed infrared, time-lapse video cameras within 5m of a nesting site in addition to daily nest checks to identify potential nest predators. We measured vegetation characteristics including visual obstruction, herbaceous, grass, litter, woody material, and canopy ground cover at each nest site and female diurnal location. We built nest survival models using AICc model selection to determine the influence of vegetation characteristics and camera. Of the 31 captured birds, 12 attempted nesting, resulting in four successful nests. We calculated that the nests have a 95% chance of survival the day after and a 32% chance of overall success. Our AICc models found no interactions among nest success and vegetation characteristics. Following nest termination of successful broods, all four broods were abandoned. Two females were radio-marked during their brood-rearing period and both broods lasted longer than 30 days of dependence. We compared the means of vegetation measurements of female diurnal locations between treated and non-treated areas and found no significant differences ($p > 0.05$). Further assessments of breeding success between treated and non-treated areas are needed to better understand the effects of restoration practices.

Citation: Belleny, D., H. Mathewson, J. Breeden, J. Tomeček, T. W. Schwertner, and J. Giocomo. 2017. Evaluation of land restoration practices on northern bobwhite productivity in Northcentral Texas—Preliminary results. National Quail Symposium Proceedings 8:240.

Key words: northern bobwhite, *Colinus virginianus*, land restoration, nest success, brood-rearing, Rolling Plains, north-central Texas

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STATISTICAL POPULATION RECONSTRUCTION USING WINGS FROM HARVESTED NORTHERN BOBWHITES CAN INFORM MANAGEMENT

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ABSTRACT

Despite the widespread collection wings from harvested northern bobwhite (*Colinus virginianus*) by state wildlife agencies and private entities, age-at-harvest information has been largely underutilized for guiding management decisions for this species. Statistical population reconstruction (SPR) techniques can use age-at-harvest information and provide a valuable tool for monitoring trends and the status of bobwhite (and other game bird) populations. However, SPR has not been applied to bobwhite. We evaluated the utility of statistical population reconstruction models, which have been applied successfully to other species (e.g., elk, *Cervus elaphus*; black-tailed deer, *Odocoilues hemonius*; and greater sage-grouse, *Centrocercus urophasianus*), to reconstruct annual abundance and demographic attributes for a bobwhite population in southwest Georgia. During 1998 – 2016, we collected wings from harvested birds ($n = 17{,}448$; $n_{annual} = 969 \pm 104$) in conjunction with survival information from mark-recapture. We derived independent estimates of fall abundance from the same site using covey call counts and a standardized measure of hunting success (coveys moved per hour). SPR models suggested that population change was stable ($\lambda = 1.00$; CV $= 0.19$) compared to moderate population growth ($\lambda = 1.05$; CV $= 0.29$) indicated by the covey call quadrat method. Abundance estimates from SPR and covey call counts were moderately correlated ($r = 0.48$) with only 3 out 18 years statistically different. Abundance estimates from SPR and hunting success (coveys moved per hour) was highly correlated ($r = 0.86$). SPR provides valid, conservative abundance estimates for bobwhite age-at-harvest data. Therefore, we endorse the use of SPR for bobwhites where age-at-harvest, hunter effort and another source of auxiliary data are readily available. As such, given that the collection of harvested wings is simple and low cost, we recommend managers and state agencies consider incorporating this technique into their management program.

Citation: Terhune II, T.M., K. M. Malone, D. C. Sisson, and J. A. Martin. 2017. Statistical population reconstruction using wings from harvested northern bobwhites can inform management. National Quail Symposium Proceedings 8:241–247.

Key words: age, harvest, *Colinus virginianus*, northern bobwhite, statistical population reconstruction, wing data

Upland game birds are important wildlife resources for most states in North America, providing substantial revenue to state wildlife programs and recreational opportunity (e.g., hunting and wildlife viewing) for the public (Burger et al. 1999). A common management objective for state and federal agencies in the United States is often to increase or maintain populations of game birds to levels consistent with the demands of consumptive and non-consumptive users (U.S. Fish and Wildlife Service 1990, Brennan and Jacobson 1992). As such, long-term population declines of several game birds such as the American Woodcock (*Scolopax minor*), the northern bobwhite (*Colinus virginianus;* hereafter, bobwhite) and the Greater Sage-grouse (*Centrocersus urophasianus*) underscores the importance of population monitoring to aid in their conservation and management, especially on public lands (Brennan 1991, Connelly and Braun 1997, Peterson et al. 2002, Schroeder et al. 2004, Link et al. 2008, Cooper and Rau 2014).

The annual establishment of hunting regulations is the product of managers understanding the population status, dynamics, and the anticipated hunting effects on

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exploited species. Reliable estimates of annual abundance, among other demographic information (e.g., harvest estimates, recruitment, etc.), is essential for guiding management decisions and conservation of a game bird species. But, these data are often lacking because they can be difficult or impractical to obtain. Several survey methods, requiring variable inputs, for estimating bobwhite abundance exist (Rusk et al. 2007, Kuvlesky, et al. 1989) such as: mark-recapture, mark-recovery, or trap-removal (O'Brien et al. 1985, Guthery 1989, Williams et al. 2001); distance sampling using covey call counts, (DeMaso et al. 1992, Seiler et al. 2002, Wellendorf et al. 2004), line transects (Brennan and Block 1986, Guthery 1988), and helicopter surveys (Shupe et al. 1987, Schnupp et al. 2013). Each of these survey techniques offer distinct advantages over the others, but many of them are limited in their application. For example, some require large amounts of data (mark-recapture) and/or are labor intensive (distance sampling, mark-recapture), expensive (helicopter surveys), or impractical at large spatial scales (e.g., covey call quadrat surveys) to implement effectively. Commonly collected by bobwhite managers, records of hunt success (coveys found per hour) have been used as an index to bobwhite abundance (Rosene 1969, Brennan et al. 1997, Stribling and Sisson 2009). Hunt success data can provide reliable trend information when protocols are standardized (Palmer et al. 2002) but they lack a measure of precision and have limited application for decision making, especially if on-site conditions change (e.g., hunting style, habitat, etc.).

In North America, however, wings from harvested game birds are often collected from hunters by wildlife agencies or can easily be incorporated into a management program. These wings provide easy-to-access information (such as age and sex) on population structure and demographic rates, which may inform management decisions when used appropriately and/or when used in conjunction with ancillary data. Age-at-harvest data can be utilized in a statistical population reconstruction (SPR) framework to derive robust estimates of population parameters, such as abundance, that may otherwise be difficult to obtain (Downing 1980, Gove et al. 2002). SPR techniques involve fitting population demographic models of harvested wildlife populations using age-at-harvest data as the primary input, an additional auxiliary source of demographic data to aid parameter identifiability (Deriso et al. 1985, Skalski et al. 2007, 2012 a, b, Clawson et al. 2013), and a measure of capture (or hunter) effort. In many scenarios, SPR can be a useful tool for monitoring long-term population trends as well as help establish harvest limits for game populations. Although SPR has been successfully applied to game species such as elk (*Cervus elaphus*; Gove et al. 2002), wild turkey (*Meleagris gallopavo*; Clawson et al. 2015), and greater sage-grouse (Broms et al. 2010*)*, it has not undergone a rigorous evaluation for accuracy in bobwhite populations.

To our knowledge SPR techniques have not been applied to bobwhite despite collection of wings from harvested birds by some state wildlife agencies and other private entities ostensibly because few techniques are readily available, or perhaps known, to incorporate such data. Given that inventorying wild bobwhite populations remains one of the greatest challenges facing state wildlife agencies, SPR may provide a useful and cost-effective tool for monitoring the status of bobwhite populations on wildlife management areas and/or focal regions comprised of either or both public and private properties. Furthermore, a salient challenge of large-scale, multi-state population recovery efforts, such as the National Bobwhite Conservation Initiative (Palmer et al. 2011), is the coordination of monitoring to provide a consistent, accurate abundance estimate using minimal data and effort across individual states. Thus, our objectives were to estimate population abundance and temporal trends in abundance of bobwhite on a private plantation located in southwest Georgia, U.S.A. from 1998-2016, and evaluate the efficacy of SPR techniques for utilizing bobwhite age-at-harvest data to estimate abundance.

STUDY AREA

We conducted the study on a private property (8,094 ha) located in Baker county in southwest Georgia, USA. The study site was located in the Upper Coastal Plain physiographic region and comprised of old field pine (*Pinus* spp.) forests (80%) with relatively low basal area (3–9 m^2/ha) and small (e.g., <2 ha), scattered fields (20%). The study area has been under intensive bobwhite management for >50 years. Habitat management techniques included frequent burning (50–70% burned annually), timber thinning, seasonal disking, chopping and mowing, supplemental feeding, and mammalian nest predator control. Typical field management consisted of disking in fall and late winter to stimulate annual weed production and arthropods. As a result of these intense management regimes, our study areas maintained abundant wild bobwhite density ranging from 2.5 to 7.4 birds per hectare (Yates et al. 1995; Burger et al. 1998, Stribling and Sisson 2009).

METHODS

We trapped wild bobwhites during October–November and March–April 1997–2016 using confusion-style, baited funnel traps (Stoddard 1931), placed at an average trap-density of approximately 1 trap per 2.56 ha. We camouflaged traps by covering them with brush (e.g., fresh-cut pine boughs) to minimize stress on captured birds. We classified bobwhites by age and sex, and we weighed, and leg-banded them with a unique identifier (#7, aluminum band from National Band and Tag) and released them at capture sites.

Harvest was conducted annually on the study site during the hunting season (November–February), contributing substantially to recovery data. Hunting was conducted from horseback, and mule-drawn wagon, using trained pointing bird dogs as well as retrieving dogs to locate lost harvested birds. The reporting rate was assumed to be 100% because we conducted this research

Table 1. Northern bobwhite age-at-harvest date for private property located in Albany, Georgia, USA, 1997 – 2007.

Year	Juvenile	Adults	Total	Capture Effort (hrs)
1998	858	247	1,105	286.25
1999	739	279	1,018	300.25
2000	1,130	327	1,457	321.75
2001	1,028	360	1,388	292.5
2002	1,098	494	1,592	339
2003	1,141	436	1,577	345
2004	1,055	551	1,606	342.25
2005	990	345	1,335	328.75
2006	666	329	995	274.25
2007	422	132	554	196
2008	582	221	803	243
2009	624	249	873	230.5
2010	550	268	818	247
2011	271	131	402	144
2012	352	94	446	179.75
2013	518	206	724	206.75
2014	214	127	341	133.25
2015	284	130	414	166.75
Total	12,522	4,926	17,448	4577

on private property, hunting and harvest was controlled, and all harvested birds was entered into a centralized research database. We constituted a year beginning on 1 October and ending 30 September of the following calendar year to fully incorporate each hunting season (November–February). Each bird harvested was handled by research staff prior to cleaning; during this time, we determined age and sex (juvenile or adult) using molt patterns on the wings (Petrides and Nestler 1943, Rosene 1969) and recorded band information if present. For each hunt, plantation staff recorded start and end times and collected information on hunt encounters (coveys pointed, coveys shot, wild flushes, etc.), number of birds harvested, covey size and number of hunters (observers). We used these data to develop capture (hunt) effort (Table 1) and deduce hunting success metrics (coveys moved per hour). All methods followed Institutional Animal Care and Use Committee approved protocol (Protocol Review No.: A1999-10028; A2001-10100; 2002-0364).

We used covey call counts (DeMaso et al. 1992, Seiler et al. 2002, Wellendorf et al. 2004) to estimate fall bobwhite abundance during 1999 – 2015. We conducted covey call quadrat surveys from mid-October through late-November and estimated bobwhite density following protocols of Wellendorf et al. (2004).

Statistical Analysis

For the SPR analysis, we used the software PopRecon 2 to construct and analyze a joint-likelihood model based on three separate likelihoods: the likelihood of age-at harvest (wing data), the likelihood of survival (mark-recapture data), and the likelihood of harvest probability (band recovery data). PopRecon 2 uses maximum likelihood estimation methods to estimate abundance for each age class and year, as well as associated confidence intervals (see Gast et al. 2013a, b). It uses a 2-stage estimation method wherein survival and harvest parameters are estimated solely based on the age-at-harvest and hunter effort data, then a Horvitz-Thompson type estimator is used to incorporate the binomial sampling process (inherent in the harvest process) into the estimates of abundance (Gast et al. 2013a, b, Horvitz & Thompson 1952).

We generated 2 types of auxiliary data for SPR: survival and band recovery data. For the auxiliary survival likelihood (mark-recapture data), we used Burnham's Live-Dead Recovery model (Burnham 1993) in program MARK to estimate survival for both age classes (juvenile and adult) in each year from 1998-2007 during which large sample sizes of banded birds were maintained. We determined age as adult ($>$1 yr) or juvenile ($<$1 yr) at time of initial capture and we assigned each individual a binary covariate. We deductively determined age for subsequent encounter occasions, whether recaptured or not, based on maturity time (Stoddard 1931, Rosene 1969). We modeled age as a time-varying indicator in MARK (using 8 indicator variables: age1, age2, age3, ..., age8) to delineate 2 groups: juveniles and adults, coded as 0 and 1, respectively. Because bobwhites were juveniles for only 1 year (i.e., 2 encounter occasions) we needed only 8 covariates (i.e., no. capture occasions/2) to model this parameter. We coded adult birds captured during spring or fall seasons as adult for the initial trapping session and each encounter occasion thereafter. We coded bobwhites classified as juveniles captured during fall as juvenile for the initial and subsequent (i.e., spring) trapping occasions and adults for remaining encounter occasions, whereas bobwhites classified as juveniles and captured during the spring we coded as juvenile for the initial trapping occasion and as adult for each subsequent encounter occasion.

For the likelihood of harvest probability, we summarized the number of individuals and banded birds recovered from harvest for each year and age class.

We used Pearson Product-Moment Correlation (R Development Core Team 2015) to measure the strength of a linear association between abundance estimates derived from covey call counts and PopRecon independently.

RESULTS

The total number of harvested birds ($n = 17{,}448$) varied by year and age class (Table 1). Average annual survival was 20.0% (SE = 3.97) and 25.24% (SE = 4.94) for juvenile and adult bobwhites, respectively (Table 2). We banded a total of 5,675 birds of which 299 were harvested during the course of the study (Table 3). Annual harvest effort was high overall ($\bar{x} = 254$ hours/year; SE = 16.63; see Table 1), but harvest effort was higher in the first 9 years compared to the second 9 years ($\overline{x_{1998-2005}} = 194.11$ hours/year; SE = 8.87; $\overline{x_{2007-2015}} =$ 194.11 hours/year; SE = 13.87, see Table 1). Similarly, hunt success (birds harvested) declined through time whereby the first 9 years (1998 – 2006) of the study an average of 4.2 birds was harvested per hour compared to

Table 2. Annual survival estimates, used as auxiliary data for statistical population reconstruction, and associated standard errors derived from Burnham's joint live-dead recovery model in program MARK for juvenile and adult northern bobwhite on a private property in Albany, Georgia, USA, 1997 – 2007.

	Juvenile		Adult	
Year	Survival	SE	Survival	SE
1997 - 1998	0.1313	0.0307	0.1434	0.0337
1998 - 1999	0.1292	0.0215	0.1828	0.0259
1999 - 2000	0.2576	0.0250	0.2922	0.0221
2000 - 2001	0.1645	0.0176	0.1886	0.0187
2001 - 2002	0.3111	0.0238	0.3978	0.0183
2002 - 2003	0.1892	0.0212	0.2147	0.0211
2003 - 2004	0.2377	0.0445	0.3303	0.0733
2004 - 2005	0.2484	0.0689	0.3193	0.0746
2005 - 2006	0.2219	0.0780	0.2426	0.0710
2006 - 2007	0.1420	0.0389	0.2539	0.0759
2007 - 2008	0.1625	0.0666	0.2116	0.1089

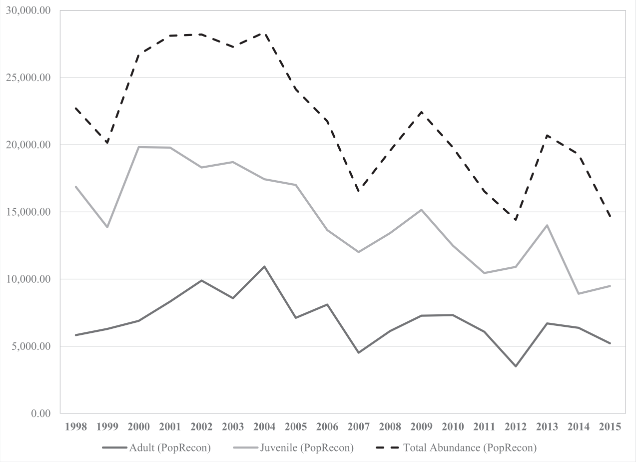

Fig. 1. Statistical population reconstruction abundance estimates for northern bobwhites (adult, juvenile and pooled) as derived from PopRecon2, during 1998 – 2015.

only 3.0 birds per hour during the last 9 years (2007 – 2015). Similarly, a banded bird was harvested approximately every 14 hours of hunting during 1998 – 2006, whereas 59 hours of hunting during 2007 – 2015 was required, on average, to harvest a banded bird (Table 1 & 3).

Using PopRecon2, we estimated the finite rate of population change to be $\lambda = 1.00$ (CV $= 0.19$) compared to $\lambda = 1.05$ (CV $= 0.29$) for covey call quadrat method. Using the fitted capture coefficient and annual adjustments to harvest effort (hours hunted), we estimated the average harvest probability of 0.0414 (SE $= 0.003$) which was similar to that estimated via program MARK, band recovery models (Terhune et al. 2007). The SPR produced reasonable annual abundance estimates for adults and juveniles (Figure 1). During the 18-year period, population reconstruction estimates from PopRecon2 and covey call counts were moderately correlated (Figure 2, $r = 0.48$); and when we removed outliers for 3 years (2007, 2012 and 2015), associated with dramatic population increases, the linear relationship increased substantially ($r = 0.71$). Population abundance estimated from SPR was more strongly correlated ($r = 0.86$) with hunt success (coveys moved per hour; see Figure 3).

Table 3. Northern bobwhite band recovery and capture effort data, used as auxiliary data for statistical population reconstruction, for a private property in Albany, Georgia, USA, 1997 – 2007.

	Banded		Harvested		Total	
Year	Adult	Juvenile	Adult	Juvenile	Banded	Harvested
1998	79	343	8	19	422	27
1999	162	639	5	32	801	37
2000	75	488	8	23	563	31
2001	125	573	11	27	698	38
2002	194	492	14	19	686	33
2003	96	204	7	7	300	14
2004	104	205	6	14	309	20
2005	73	234	4	13	307	17
2006	92	161	0	11	253	11
2007	30	106	0	4	136	4
2008	29	97	1	3	126	4
2009	31	106	1	8	137	9
2010	52	82	5	3	134	8
2011	28	79	0	6	107	6
2012	39	76	1	3	115	4
2013	32	64	1	1	96	2
2014	34	60	0	1	94	1
2015	24	61	0	0	85	0
Total	1346	4329	76	223	5675	299

DISCUSSION

Statistical population reconstruction appears to be a promising tool for estimating bobwhite abundance using age-at-harvest data. We found that SPR provided more conservative abundance estimates during most years compared to fall covey call counts such that evaluation

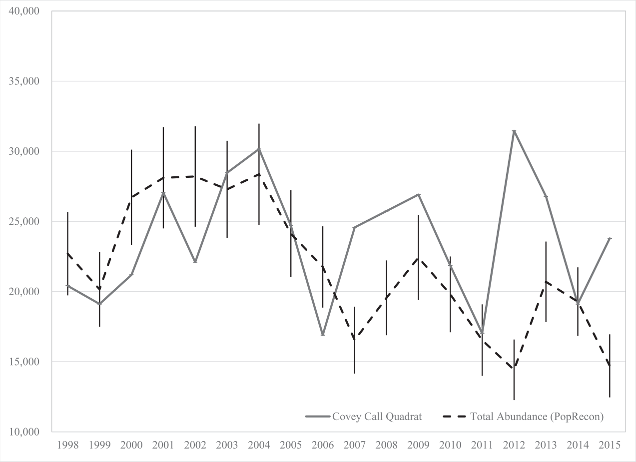

Fig. 2. Annual abundance estimates for northern bobwhites derived from statistical population reconstruction using PopRecon2 and covey call counts, during 1998 – 2015.

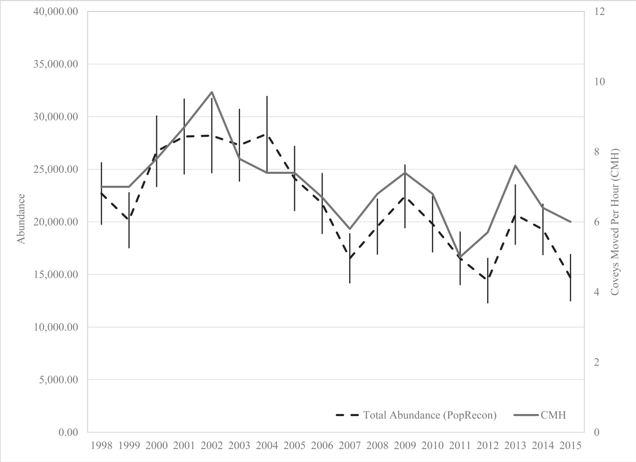

Fig. 3. Annual abundance estimates for northern bobwhites derived from statistical population reconstruction using PopRecon2 and hunting success represented as coveys moved per hour, during 1998 – 2015.

of these estimates inferred a stable population whereas traditional covey counts suggested a slightly growing population (4.6% increase per year). Covey call counts occurred on a small subset (<10%) of the study area whereas harvest of bobwhites occurred throughout the property potentially explaining some of the disparity among population estimates. SPR has been suggested to provide a minimum population estimate as opposed to true abundance (Davis et al. 2007), but further evaluation and comparison to other population estimation techniques (e.g., mark-recapture, Lincoln-Peterson) is warranted.

Annual trends from SPR may be misleading in certain years when annual survival or recruitment rates are highly variable (outside the long-term averages) over time as they can be for high-turnover species such as bobwhites. For example, during 3 years (2007, 2012, and 2015) where dramatic population increases occurred in covey call data, SPR abundance estimates differed from covey call estimates by more than 8,000 individuals. However, the strong relationship between hunt success (coveys moved per hour; Figure 3) and SPR abundance estimates suggests that bias associated with covey call counts is a plausible explanation for the difference during these 3 years. For instance, in 2007, the property was hit by a severe tornado which was debilitating to habitat in the area immediately followed by a new ground effect related to cleaning up with heavy equipment after the event (Palmer et al. 2000, Sisson et al. 2002). This new ground effect elicited a rapid bird response on a portion of the census plots, elevating population estimates for the area impacted. If SPR is insensitive to sharp upticks in abundance, inclusion of recruitment auxiliary data, such as broods produced per hen or chick survival, could help to mitigate this bias and inform the models for improved estimation (Gast et al. 2012). Davis et al. (2007) submitted that collapsing age classes was highly effective and provided more robust abundance estimates in these cases, but also recognized that certain violations of assumptions are known to impact abundance and trend estimates which might explain the difference we observed in 3 years experiencing precipitous population growth. Alternatively, because bobwhite wings from harvested birds can be backdated to incorporate multiple juvenile age categories (e.g., 1-month, 2-months, 3-months; see Rosene 1969, Petrides and Nestler 1943), improved reconstruction estimates during rapid population expansion years is plausible.

Beyond age-specific abundance, SPR provides demographic parameters such as probability of harvest, survival and recruitment that could inform management decisions or regulatory processes through adaptive management or complement harvest information programs (HIP). For instance, one could ostensibly use this method to determine which demographic (e.g., recruitment or harvest) is limiting population growth and potentially adjust management or harvest regulations accordingly (Skalski et al. 2011). In our study, probability of harvest was relatively constant and low (<%7), suggesting that recruitment and/or variation in annual survival was likely driving population fluctuation from year to year and not additive harvest mortality. In a similar vein, using SPR to investigate the sensitivity of hunter effort relative to known demographics such as natural mortality and harvest rate may help to establish hunting regulations or adjust bag limits. We observed, for instance, that for every hour of hunting during the first 9 years (1998 – 2006), 4.2 birds were harvested compared to only 3.0 birds harvested per hour of hunting during the last 9 years, suggesting hunt success was lower during 2007 – 2015. Numerous factors could explain this decline in hunt success such as inexperienced hunters, variable climate or variable scenting conditions, or changes in vegetation density. Although hunting effort (total hours hunted per year) remained high from year to year, we observed a lower proportion of banded birds harvested later (2007 – 2015) in the study due to a change in hunter demographics which may have contributed to lower estimated abundance from SPR during some years. The interplay between hunter effort and hunter success (harvested birds) on SPR abundance estimates merits additional research.

In this study, we demonstrated the utility of SPR models in estimating bobwhite abundance, yet these models could still be improved with additional or different types of auxiliary data. In addition to harvested wing data, many agencies collect auxiliary data on bobwhite such as visual counts (e.g., mail route counts, coveys moved, broods seen), offspring observed per adult bird, band-recovery, mark-recapture or telemetry data rendering this technique broadly applicable across the range of bobwhite. Various auxiliary inputs likely influence demographic estimation and precision differently, substantiating the need to further investigate how sensitive these models are to specific auxiliary data as well as to better understand the limitations to lack of temporally and spatially comprehensive datasets for the period/area of interest. For example, while an agency may procure multiple years of age-at-harvest data from hunter harvested wings, auxiliary data may only be necessary for a subset of those years in order to obtain reliable SPR estimates. Given the successful application of SPR, we recommend its use for bobwhites, particularly on areas too large to conduct covey call counts, and where age-at-harvest and other auxiliary data are available.

MANAGEMENT IMPLICATIONS

Statistical population reconstruction is a relatively easy, low effort technique which takes advantage of data (age-at harvest, hunter effort) already being collected on many public lands; and, SPR provides the added benefit of a measure of precision, unlike some other techniques (e.g., coveys moved or seen per hour hunted). Thus, the use of SPR provides land managers with a credible and defensible means for developing conservative harvest strategies while ensuring long-term population persistence and recreational opportunity (Skalski et al. 2011). Use of wings from harvested birds also involves hunters in research and management through citizen science. As such, and if not already doing so, we urge state agencies to consider collection of harvested wings as a low-cost monitoring tool to help adaptively inform management.

Deliberate collection of auxiliary information over time, will enhance the use of statistical population reconstruction models to inform conservation and management of bobwhites on public and private lands. Careful planning by state wildlife agencies can provide improved estimation of abundance and further aid in making management decisions or setting harvest regulations through use of SPR. The extension of local auxiliary data to be broadly applied to regional areas offers promise but needs to be further tested. Large-scale conservation efforts, such as the National Bobwhite Conservation Initiative (Palmer et al. 2011) and the Coordinated Implementation Plan, could structure data collection to inform target population densities from archived data or develop abundance measures across the range using SPR to evaluate successful habitat management implementation.

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USE OF SPRING WHISTLE COUNTS TO PREDICT NORTHERN BOBWHITE RELATIVE ABUNDANCE

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ABSTRACT

Spring whistle counts are commonly used to index northern bobwhite (*Colinus virginianus*) breeding populations and make inference about relative autumn abundance. They are relatively cheap and easy to implement and provide the advantage of surveying bobwhite populations from multiple points daily and early in the year. This could prove useful on properties available for potential lease, purchase, or as translocation sites; as well as to monitor population trends. Our objective was to determine whether spring whistle counts reliably forecast autumn covey numbers on a wide range of sites, years, and densities on 6 properties in southwestern Georgia from 2006 to 2015. We conducted spring whistle counts weekly during peak calling activity (late May–early Jun, for 4–6 consecutive years) on an average of 7 points/property (range = 5–9). We conducted autumn covey counts using these same sampling points as an index of relative abundance. Peak number of males heard in spring and number of coveys heard in autumn was strongly correlated ($R^2 = 0.791$, $n = 198$) for all points combined, indicating that spring whistle counts are a reliable tool for assessing bobwhite relative abundance on sites where autumn covey counts are precluded or the information is needed prior to autumn.

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Key words: Colinus virginianus, covey counts, Georgia, northern bobwhite, translocation, whistle counts

Spring whistle counts have been used by researchers and managers for decades as an index to spring breeding-population levels of northern bobwhites (*Colinus virginianus*) and have been evaluated extensively as a way to predict autumn population densities with varying results (Speake and Haugen 1960, Norton et al. 1961, Robel 1969, Rosene 1969, Wells and Sexon 1982, Curtis et al. 1989, Hansen and Guthery 2001, Terhune et al. 2009, Parent et al. 2012, Reyna et al. 2012). More recent work demonstrated a strong relationship ($R^2 = 0.975$) between spring whistle counts and autumn density, derived from covey call counts, when the peak of spring whistling activity is used (Terhune et al. 2009). Peak male whistling activity occurs more than once during the nesting season, coincides closely with peak nesting activity by hens, and varies by year and site (Hansen and Guthery 2001, Terhune 2002, Terhune et al. 2009). The most consistent and intense peak was during week 7–9 of the nesting season in South Georgia (late May–early Jun; Terhune 2002). Additional studies have shown that calling activity during this time period is more consistent than either before or after (Wellendorf and Palmer 2012). Terhune et al. (2009) underscored the need to test the validity of their findings on more sites and with a wider range of densities to better inform management and a broader use of the technique.

The value of predicting autumn population levels of bobwhites prior to ($\geq$6 months) hunting season has several advantages such as to afford managers a practical and reliable method to forecast quail numbers to set lease hunting prices (Reyna et al. 2012) or establish conservative bag limits or quota permits. In the southeastern United States, we have often been asked to evaluate properties for potential lease, purchase, or as a suitable translocation site in advance of the season appropriate for accurate covey census. Given the great deal of time and effort going into a translocation project, knowing in advance whether a property meets the minimum population requirements for permitting is very valuable (Terhune et al. 2009). Part of the translocation permitting process required by the Georgia Department of Natural Resources, Wildlife Resources Division (GA DNR WRD), and several other states, was to conduct both spring whistle counts and autumn covey counts on translocation recipient sites. This provided us with the opportunity to compare these counts on multiple sites, over multiple years, and over a wide range of densities to evaluate the utility of spring whistle counts as a valid metric for assessing relative autumn abundance.

STUDY AREA

We conducted both spring whistle counts and autumn covey counts on 6 study sites in 6 different counties in

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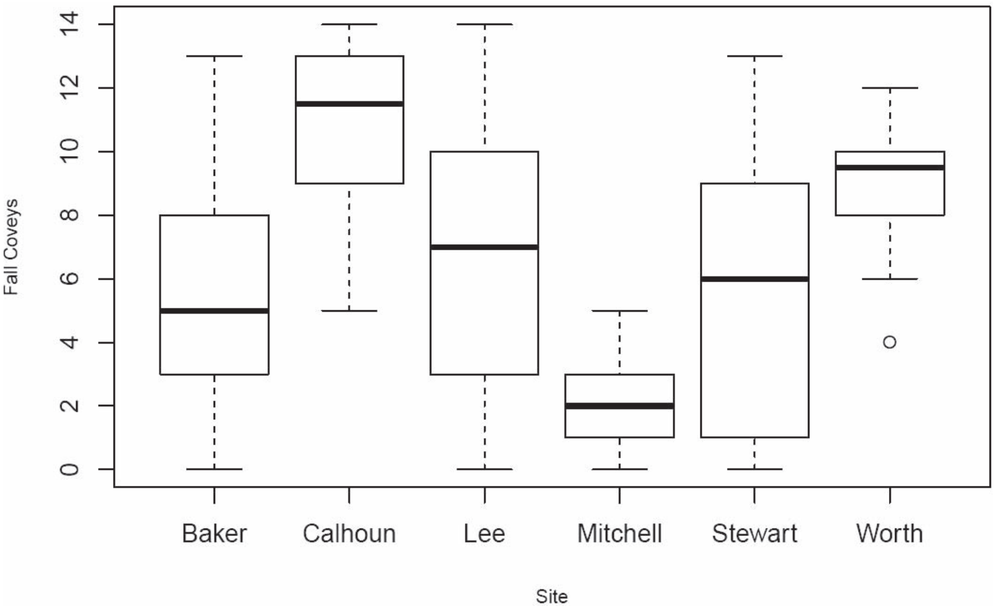

Fig. 1. Average number of northern bobwhite coveys heard delineated by site during October–November on 6 sites in southwestern Georgia, USA, 2006–2015.

southwestern Georgia (Fig. 1). Two sites located in Calhoun and Worth counties had a long history of intensive quail management and relatively high densities of bobwhites whereas the other 4 sites located in Stewart, Baker, Mitchell, and Lee counties were either newly established or renovated wild quail hunting properties with a more recent history of wild quail management and a low initial quail density. All 6 sites were managed intensively for wild quail throughout the study as described by Stribling and Sisson (2006), including maintaining open canopy pine (*Pinus* spp.) forests with frequent prescribed fire, mowing and roller chopping, herbicides, and disking of fallow openings, along with predator management and supplemental feeding of quail. Spring whistle and autumn covey counts were initiated on each site because of new owners and their desire to measure the bird numbers prior to purchase, in response to newly implemented management regimes, or as translocation monitoring as required by GA DNR WRD.

METHODS

Spring Whistle Counts

We followed the protocol of Terhune et al. (2009), which was based on previous research on male calling behavior (Ellis et al. 1969, Rosene 1969, Wells and Sexon 1982, Curtis et al. 1989, Hansen and Guthery 2001) to ensure accurate counts and to mitigate the influence of weather (i.e., wind, fog, rain, and cloud cover) on whistling males. We conducted numerical counts of whistling males along standardized call count routes each week at 5–9-day intervals (mid-May–mid June) during 2006–2015. We counted the number of individual males heard whistling during the first 2 hours after sunrise, the "calling optimum" (Rosene 1969, Hansen and Guthery 2001), on days when the wind velocity was ≤16 km/hour and cloud cover was ≤75%. Spring whistle count routes comprised an average of 7 listening points (range = 5–9), 0.81 km apart, evenly distributed throughout the study area. The observer stopped and listened for 5 minutes at each point and recorded the start time; number of whistling males; and climate conditions such as wind speed and direction, cloud cover, or fog. We ran the spring whistle-count route backward on alternating weeks to decrease bias of optimal calling time and listening point locale. We used the peak number of males heard whistling at each point in the analysis.

Autumn Covey Counts

We used autumn covey counts (DeMaso et al. 1992, Seiler et al. 2002, Wellendorf et al. 2004) to evaluate autumn covey numbers during 2006–2015. We conducted autumn covey counts from mid-October to late-November. We used point count techniques to estimate bobwhite covey numbers where a single observer listened for the "koi-lee" covey calls (Stoddard 1931) given by bobwhites before sunrise and recorded the unique number of calling coveys. We conducted autumn covey counts using the same points as those used for the spring whistle counts, repeated each 2–3 times, and used the high count from each point for analysis (Wellendorf et al. 2004).

Statistical Approach

We used generalized linear models (R Core Team 2015) to estimate effects of peak spring whistle counts during the breeding season, site, and year on the peak numbers of calling coveys in the autumn. For our analysis, we were most interested in determining whether the number of whistling males during the peak of spring calling was correlated with the number of distinct calling coveys in the

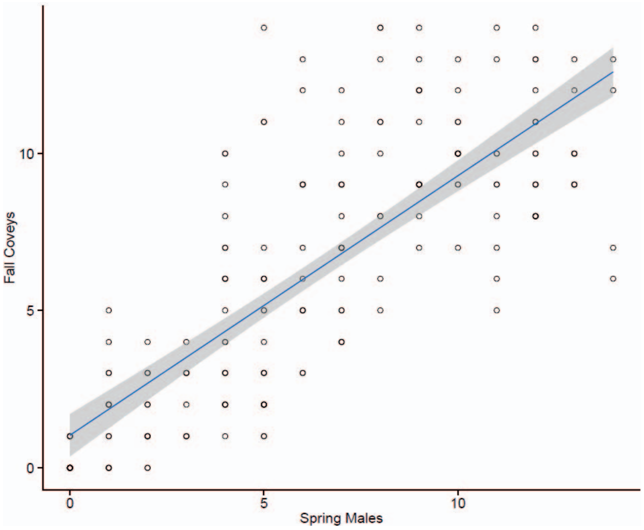

Fig. 2. Generalized linear regression model using the peak of northern bobwhite calling activity plotted with prediction limits for 6 study sites in southwestern Georgia, USA, 2006–2015. Regression equation and coefficients: y = 1.03289 + 0.82589 × (Spring Northern Bobwhite Count); $R^2 = 0.791$.

autumn. As such, we controlled for variation in year and site by including these terms in our models. To facilitate interpretation of regression coefficients, we standardized the continuous predictors and the response variable by unit normal scaling (Montgomery and Peck 1992).

We used an information-theoretic approach (Anderson et al. 2000, Burnham and Anderson 2002) to evaluate a set of 7 candidate models describing breeding season calling of bobwhite males compared with autumn covey counts. We determined the best approximating model in the set of candidate models by Akaike's Information Criteria (AIC; Burnham and Anderson 2002). We used model likelihoods computed from Program R (https://www.r-project.org/; R Core Team 2015) to compute AIC and compare each candidate model. We considered the model with the lowest AIC value to be the best approximating model given the data. We assessed model fit by model coefficient of multiple determination (R^2) and mean squared error. We also evaluated model fit using residual analysis where sample size was adequate. During initial model fitting, no intercept models of bobwhite abundance predicted from counts of breeding calling males were found to best fit the data.

RESULTS

The examination of residual plots suggested the fit for the most highly parameterized models evaluating the effects of male calling activity, year, and site on autumn coveys heard was acceptable. Visual observation of normal probability plots revealed some slight departure from normality for all of the models, but this departure was not severe (Hosmer and Lemeshow 2004). Based on these model residuals plotted against residual values, we assumed that the fit of the most highly parameterized models and the fit of subsequent candidate models also was adequate.

Table 1. Model selection results for examination of factors (year, site, and males calling in the spring) affecting northern bobwhite covey calls heard during the subsequent autumn on 6 sites in southwestern Georgia, USA, 2006–2015.

Model	K	Dev	AIC	ΔAIC
MH[a] + MH × site[b]	12	892.7354	908.74	0.00
MH + site	8	879.2602	911.26	2.53
MH + site + year[c]	16	858.7636	918.77	10.03
MH + site + year + site × year	30	899.1107	921.11	12.38
MH + year	11	896.0564	936.06	27.32
MH + MH × year	20	932.256	936.26	27.52
MH	2	939.3894	939.39	30.65

[a] No. males heard.
[b] Site indicates all 6 sites.
[c] Year indicates all 10 yr of the study.

The average number of coveys heard in the autumn across all sites and years combined was 6.268 (SE = 0.042) and ranged from 0 to 14, representing a wide range of bobwhite densities (Fig. 1). The most supported model among those evaluated included males and site, suggesting that variation in the number of coveys heard in the autumn was largely associated with the number of whistling males in the spring and varied by site (Table 1; y = 1.03289 + 0.82589 × (Spring Northern Bobwhite Count). There was virtually no support for any of the remaining candidate models or year based on model weights and AIC (Table 1). The number of bobwhite coveys heard in the autumn was highly correlated ($R^2 = 0.791$; Fig. 2) with the peak number of males whistling in the spring. The magnitude of the slope or strength in this relationship, however, varied by site (Fig. 3).

DISCUSSION

Our results indicate that spring whistle counts are a reliable predictor of autumn covey numbers in our area when counts are conducted properly. Repeating spring whistle counts and ascertaining the peak number of whistling males during each year likely increases the utility of spring counts (Terhune et al. 2009). This is an important point because calling activity varies by year, within a season, and across sites (Hansen and Guthery 2001, Terhune 2002, Terhune et al. 2009). To accurately depict spring breeding numbers point counts must coincide with peak female nest incubation, which is an important variable driving the variability of fluctuating whistling activity (Terhune 2002, Terhune et al. 2009).

The utility of spring whistle counts have been criticized in the past largely because they do not directly incorporate information on reproductive success and seasonal survival (Norton et al. 1961). Our results indicate a consistent relationship between spring whistle counts and autumn covey counts where reproductive effort is generally consistent from year to year. However, in more arid and weather-driven portions of the bobwhite range, this relationship may be less reliable (Reyna et al. 2012). For example, Parent et al. (2012) found a fairly significant

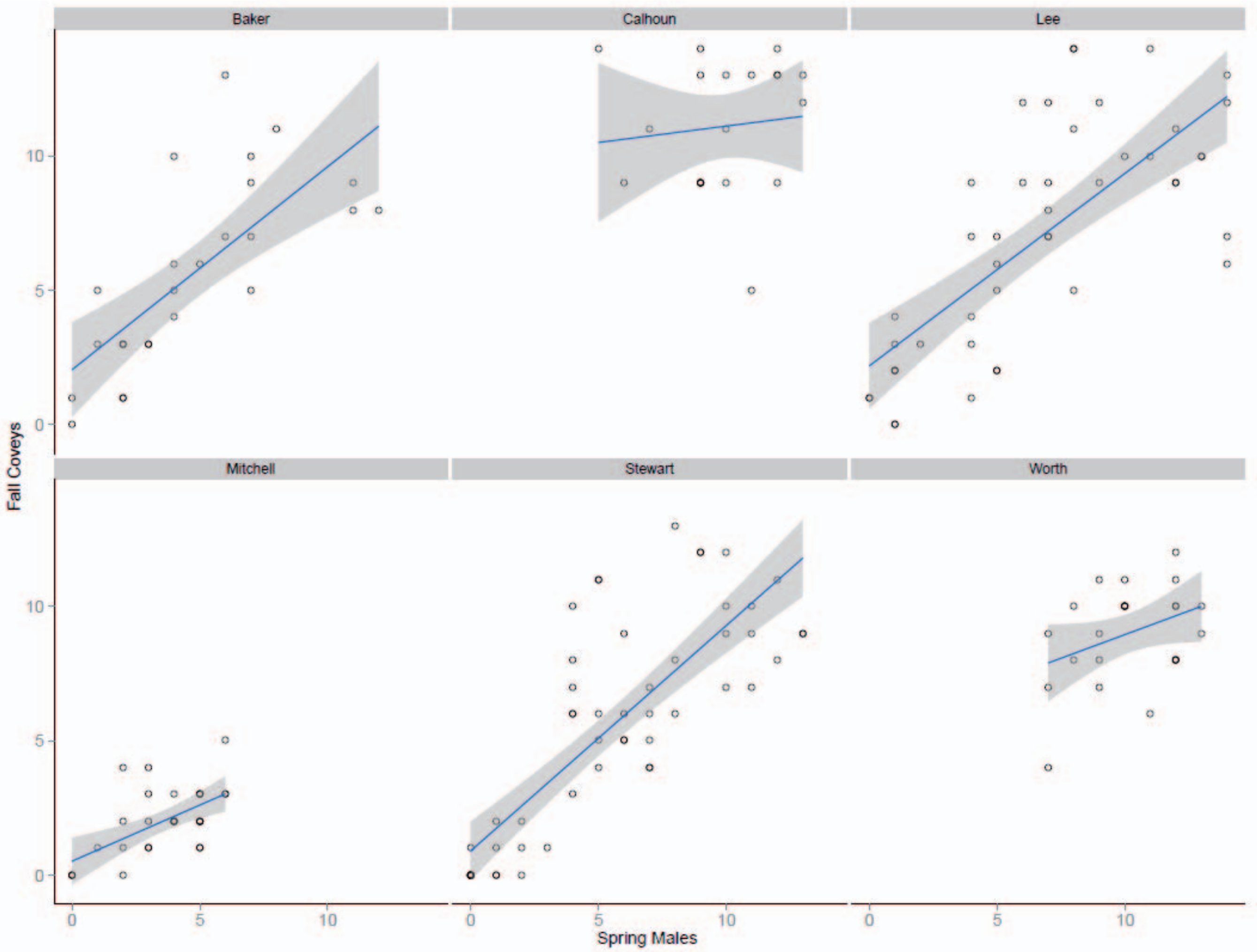

Fig. 3. Generalized linear regression model using the peak of northern bobwhite calling activity delineated by site and plotted with prediction limits for 6 study sites in southwestern Georgia, USA, 2006–2015.

relationship ($R^2 = 0.68$) in Texas between spring whistle counts and autumn helicopter surveys, whereas Reyna et al. (2012) did not ($R^2 = 0.41$). In relatively stable weather environments, such as our studies in the Deep South, it makes sense that spring whistle counts ostensibly have more predictive power ($R^2 = 0.791$).

Overwinter survival and available breeding birds have long been considered important to subsequent autumn populations (Stoddard 1931). More recent analysis of the sensitivity of populations to demographic parameters has reinforced this notion (Sandercock et al. 2008). It is logical then that having an accurate measure of spring breeding numbers would have some bearing on the subsequent autumn population. By doing repeated counts with experienced observers we were able to get accurate counts of peak calling numbers each year during the most consistent time of calling activity in both spring and autumn. These results seem to verify Rosene's findings from decades ago that each whistling male heard in the spring would represent a covey in the autumn (Rosene 1969), although his point counts were conducted haphazardly as convenient sampling during spring and summer.

The variation explained by site in our results is not unexpected because there was a wide range of initial densities on our study sites (Fig. 1). Although some sites started with virtually zero birds, others had 8–10 males whistling on some points. Higher density sites experienced more subtle increases in population growth while other sites observed dramatic increases during the course of the study. The relationship of spring whistle counts to autumn covey counts on high-density sites may not be as reliable compared with lower density sites. The presence of conspecifics calling elicits more calling activity whereby higher densities of whistling males results in higher calling rates (Wellendorf and Palmer 2012). On some of our study sites male whistling density was high (>10 birds calling/point), rendering it difficult to discern individual whistling males. This might reduce one's ability to report accurate numbers, supporting previous findings by Ellis et al. (1972). Although our sample size was lower, we observed higher variation in point-count estimates at higher densities, suggesting that the technique may be more appropriate and more meaningful when measuring lower densities (<1 bird/acre) or tracking population increases to get to high density. At higher densities the quadrat method of covey census is more dependable (Wellendorf et al. 2004); however, the need to switch to this method because of density is already indicative of some level of success. These findings are important and novel because previous studies did not incorporate such a wide range of sites with varying population density and, thus, were unable to address the performance of using spring whistle counts in varying bird densities. More research is needed to better understand if this relationship holds up at higher densities.

The lack of support for annual variation as a predictor in our study may be attributed to the lack of dramatic population growth observed temporally in the southeastern United States compared with other boom-and-bust type populations. We do not typically observe the dramatic annual swings in populations such as occur in more weather-driven populations in the bobwhite range to the west or north. As such, spring whistle counts in these environments have not been shown to be as reliable of a predictor of autumn populations or breeding activity (Bridges et al. 2001, Reyna et al. 2012).

MANAGEMENT IMPLICATIONS

Our results indicate spring whistle counts are a reliable tool in the Deep South of the United States for predicting autumn covey numbers for purpose of lease, purchase, or translocation eligibility as long as the counts are done correctly (i.e., at peak of calling activity). We recommend that counts should be conducted by experienced observers and repeated weekly to ascertain the peak number of calling males from each point for comparison from year to year and across sites. The timing of spring whistle counts provides an advantage over autumn covey counts to forecast baseline autumn population abundance to meet permit requirements for translocation (such as that stipulated in the GA DNR WRD permitting requirements). However, given that peak spring whistle counts are a predictor and not an actual estimate of autumn abundance, we do not recommend establishing bag limits from this method but rather using other methods to estimate autumn abundance for these purposes.

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RETENTION AND EFFICACY OF CITIZEN SCIENTIST VOLUNTEERS OF THE TEXAS QUAIL INDEX

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ABSTRACT

The Texas Quail Index (TQI) was a 5-year, science-based project that utilized citizen scientists to collect data in the field, including 5 indices of bobwhite abundance in the spring, and 3 indices of bobwhite abundance in the fall. Over the course of the study, 84% of all volunteers dropped out of the program and <8% of all data sets were complete. Accordingly, we surveyed the volunteers by mail to determine the rate and cause of participation decline and to identify characteristics of a reliable volunteer. Results indicated that annual volunteer participation rate declined more rapidly as time and labor requirements increased. Similarly, 74.3% of survey respondents who dropped out of the study reported leaving because the project required too much time and work. Motives may have contributed to the volunteer attrition as 72% of volunteers joined the program to learn more about quail management; however 71% of those that left the program reported not gaining knowledge in that area. We recommend that project designs, for citizen-science projects, should incorporate the motives of volunteers and recruit those whose motives best align with project goals. We also recommend that citizen-science coordinators keep volunteer tasks short and within the interest of the volunteer, to increase retention. Finally, we recommend stipends for volunteers on large-scale, laborious projects.

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Key words: citizen science, *Colinus virginianus*, management, motives, northern bobwhite, project design, quail abundance, science, Texas, volunteers.

INTRODUCTION

Citizen-science involves volunteers from the general public gathering data for use by scientists to investigate questions of research importance (Trumbull et al. 2000, Silvertown 2009). Citizen-science programs were established initially as a tool to educate the public about the scientific process (Brossard et al. 2005), but are used increasingly for surveying and monitoring animal populations (e.g., Christmas Bird Count; Lepczyk 2005, Devictor 2010). This trend is likely due to their practicality and affordability in projects where the collection of data is large-scale, time-sensitive, and funding is limited (Altizer et al. 2004). Although practical and affordable, debate continues on whether using citizen scientists is efficient (Irwin 1995, Fore et al. 2001, McCaffrey 2005).

Citizen-science project coordinators seek to recruit volunteers who are reliable and who provide useful data throughout the study; however, the volunteer aspect of citizen-science often results in participants who are initially excited about participating but later drop out of the program (McCaffrey 2005, Rotman e al. 2012, Nov et al. 2014). This pattern was observed with volunteers of the Texas Quail Index (TQI), a 5-year citizen-science project that assessed the relationship between 5 potential predictors of bobwhite abundance in the spring (spring cock-call counts, forb species richness, simulated-nest fate, potential nest-site density, and scent station visitation rates) and 3 indices of bobwhite relative abundance in the fall (roadside counts, fall covey-call counts, and harvest data). The goal of the TQI was to determine if fall quail abundance could be determined by spring predictors (Reyna et al. 2012). An enticement to volunteers and an ulterior goal of the TQI was for citizen scientists to learn more about quail in their area through participation in the project. As a result, 76 volunteers participated in the project over the 5-year period with varying reliability and effectiveness (Reyna et al. 2012).

Several studies characterized different publics (e.g., landowners, hunters) based on their willingness to cooperate in land and wildlife management programs (Raedeke 2001, Sanders 2005, and Wagner et al. 2007). Others have evaluated the motivations and values of citizen scientists in general (Hayghe 1991, Clary et al. 1996, Rotman et al. 2012). One factor common among these studies is that no definitive typology has been determined for a citizen scientist who reliably collects relevant data; thus, the aim of this study was to survey TQI participants to determine motives for engaging and disengaging the program and to identify characteristics of a reliable volunteer so that future citizen-science coordi-

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nators can better recruit and retain volunteers who provide reliable data.

METHODS

Citizen Scientist Characteristics

A mail survey was administered to all volunteers of the Texas Quail Index ($n = 76$) to acquire information regarding their motives for participation, demographics, participant satisfaction, and land ownership goals. The questionnaire was approved by the Texas A&M Institutional Review Board (Protocol number: 2007-0214) and followed Dillman's (2007) Total Design Method which incorporates a personalized multiple mailing approach to achieve an ample response rate for statistical analysis (Dillman 1991).

Initially, pre-survey letters were mailed (day 1) to all volunteers informing them of the forthcoming questionnaire. On day 5, 76 questionnaires were mailed in color print with self-addressed stamped envelopes, followed by 70 post cards (excluding 6 invalid addresses), serving as a thank you or reminder, on day 12. Another black and white questionnaire with self-addressed stamped envelopes was sent to non-respondents only, on day 19. Finally, a concluding postcard (serving as a thank you or reminder) was sent to non-respondents on day 26. All correspondence was personalized by addressing each volunteer by name and by including the signature of the Texas Quail Index coordinator with whom the volunteers were familiar.

Citizen Scientist Participation Rate

Project participation rate is typically shown as a bar graph but such graphs only illustrate the number of total participants each year and lack important information such as the actual time (e.g., month or quarter) participants immigrated to, or emigrated from, the program. Therefore, we first used the Kaplan-Meier Log Rank Analysis (Kaplan and Meier 1958) to determine differences in participation rate among volunteer cohorts (groups trained and starting in the beginning of each year). Subsequently, we used the Kaplan-Meier procedure with modifications from Pollock et al. (1989) to more accurately display the timing of participant decline. Each year of the TQI project was divided into quarters for time scale since harvest-data collection ended in the first quarter and new participants began work in the second quarter of each year (Reyna et al. 2012). For this procedure (modified Kaplan-Meier), we did not censor any volunteers; we only recorded their status as "out of TQI" or "new to TQI". We recorded the number "at risk" as the number of volunteers available for data collection at the beginning of each quarter.

Statistical Analysis

We used SigmaPlot version 12.3 (San Jose, California, USA) to analyze data from the mail survey. Shapiro-Wilk tests for normality were performed on all data sets and t-tests and Mann-Whitney Rank Sum tests were used to analyze differences in motivations, demographics, satisfaction, and landownership goals between those that dropped out of the program (Disengaged), and those that did not (Engaged; Ott and Longnecker 2001). We then conducted logistic regressions to determine which of 9 independent variables predicted whether or not respondents stayed in the program and collected accurate data. Dependent variables were dichotomous ($1 = \text{yes}$, $0 = \text{no}$) and included "Stayed in the Program" and "Collected Accurate Data"; both questions were asked in the survey. Independent variables included Age (continuous), Role ($1 = \text{Landowner}$, $2 = \text{Agency Biologist}$, $3 = \text{Other}$), Previous Citizen-Science Experience (Experience; $1 = \text{yes}$, $0 = \text{no}$), Education ($1 = \text{High School Diploma}$, $2 = \text{College Diploma}$, $3 = \text{Graduate Diploma}$), Previous Wildlife Courses ($1 = \text{yes}$, $0 = \text{no}$), Member of Conservation Organization ($1 = \text{yes}$, $0 = \text{no}$), Motivation to Join ($1 =$ to learn more about quail management, $2 =$ to contribute to scientific data, $3 =$ for fun, and $4 =$ other), Overall Satisfaction with Program ($1 = \text{yes}$, $0 = \text{no}$), and Increased Knowledge in Quail Management ($1 = \text{yes}$, $0 = \text{no}$). We used an alpha of 0.05 to determine statistical significance.

RESULTS

Citizen Scientist Characteristics

Total response rate was 84.3% ($n = 59$ total respondents; 39 Disengaged; 20 Engaged), which included 61.4% response rate for the initial questionnaire, 1.4% for the following post card, 20.0% for the second questionnaire, and 1.4% for the final reminder. Demographic variables did not differ between Disengaged, and Engaged respondents ($P > 0.05$ for age, gender, education, and occupation). Average age for all volunteers was 49 years (± 13.8; standard deviation). Males comprised 93% of respondents, 85% had a college degree, 40% were landowners, 55% agency biologists, and 5% interested volunteers.

The TQI experienced a high turnover rate where 66.1% of all participants left the program (Reyna et al. 2012). Most of the Disengaged survey respondents (61.5%) reported that they left the program because it took too much of their time; 20.5% said they changed jobs and left the area (all agency biologists); 12.8% said it required too much work, and 5.1% believed the data they collected did not matter.

Motivation to join the project did not differ between Disengaged and Engaged respondents ($P = 0.502$) where 72% of respondents joined to learn more about quail management, 11% to contribute to scientific data, 9% thought it would be fun, and 8% said it was recommended as part of their job (all agency biologists). Education and previous experience in citizen-science programs did not differ between groups ($P = 0.545$ and 0.186 respectively). Only 15% of respondents reported previous citizen-science experience, and most (92%) completed at least 1 wildlife course (college or workshop) prior to participating in the TQI.

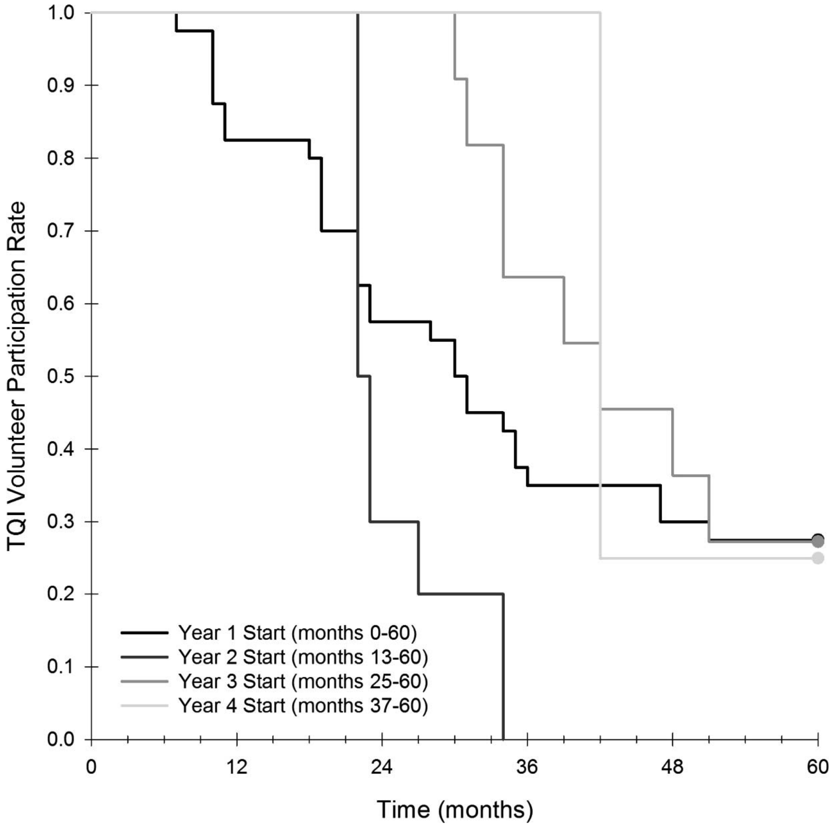

Fig. 1. Kaplan-Meier survival curves illustrating the volunteer participation rate of the Texas Quail Index citizen science project, 2002–2006. Individual curves represent a cohort of volunteers starting each year of the project and their participation rate for the duration of the project. Legend parentheses show potential participation time for each cohort. Time is divided by months and quarters of the project.

Overall satisfaction with the program did not differ between Disengaged and Engaged respondents ($P = 0.163$). Most respondents (75%) were satisfied with communication from TQI coordinators, 85% with quality of training and personal benefits, and 90% said they were satisfied with the overall experience.

Landownership goals were also not different between Disengaged and Engaged participants ($P = 0.695$). Half of sites were used for ranching (50%), 28% hunting, 14% research, and 8% pleasure. Of all sites, 33% reported participating in a landowner incentive program (i.e., an incentive program usually funded by a governmental agency designed to assist landowners in protecting or managing rare species).

When assessing the ulterior or secondary goal, "learning more about quail in your area", more Disengaged participants (71%) reported that they did not increase their knowledge in one or more aspects of the program as compared to 47% of Engaged participants ($P = 0.021$). Combined, participants agreed they learned more about quail abundance estimation, plant identification, habitat evaluation, food sources for quail, quail nesting success, quail calls, and quail locations on associated property. Participants reported they did not increase knowledge in predator abundance estimation, quail response to management actions, or quail biology.

Separate logistic regression models were not statistically significant for each of the dichotomous dependent variables, "Stayed in the Program" ($X^2 = 60.076$, $P = 0.113$) and "Collected Accurate Data" ($X^2 = 39.433$, $P = 0.806$) along with the 9 independent variables.

Citizen Scientist Participation Rate

A Kaplan-Meier Log Rank Survival Analysis with multiple comparisons showed that participation by the volunteer cohort in year 2 of the TQI (2003) was different than all other years, where all year-2 participants dropped out of the program ($P < 0.001$; Figure 1). Further, a modified Kaplan-Meier survival analysis using a cumulative participation rate of cohorts showed that participation rate declined significantly in the 3rd and 4th quarters of each year except year 4 where participation began declining in quarter 2, and in year 5 where participation rate was steady. However, year 5 cohorts did have some disengaged participants (Figure 1) but individuals from previous cohorts stayed engaged resulting in a steady participation rate for that year (Figure 2). Combined, both analyses demonstrate that recruitment and retention declined over all 5 years.

DISCUSSION

The high response rate to the TQI questionnaire (84.3%) was more than sufficient to overcome non-response bias (Dillman 1978), especially without the use

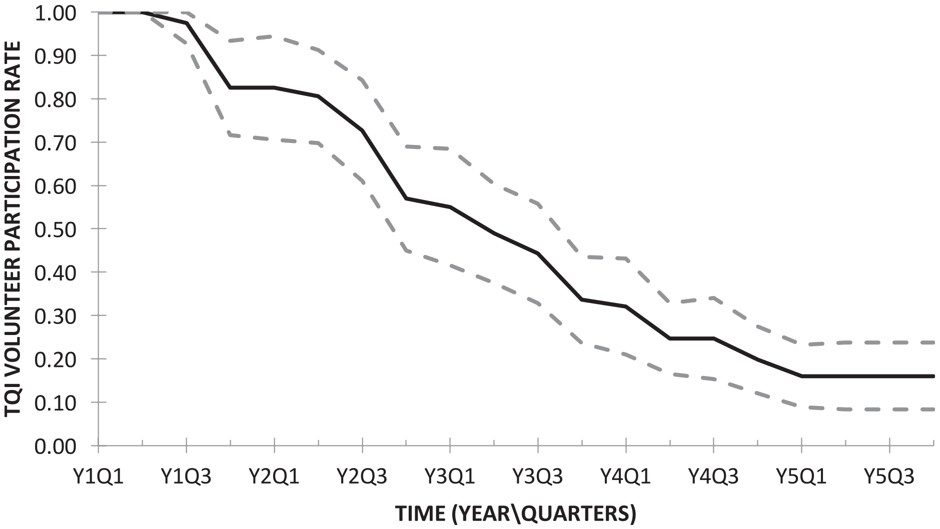

Fig. 2. Kaplan-Meier survival curve illustrating the volunteer participation rate of the Texas Quail Index citizen science project, 2002–2006. Time is divided by years and quarters. Dashed lines represent 95% confidence intervals.

of an incentive to respond (Dillman 2007). This was likely realized because of several factors. Although many TQI participants left the program, the nature of their bond with Texas AgriLife Extension remained through other programs and workshops. With branded envelopes and letterhead, the response rate could have been high simply because of familiarity and trust (Dillman 2007). The professional style of the survey documents (i.e., personalized greetings, color print, and personal signature) likely represented that relationship in a positive manner and may have made a better visual impact on volunteers than a standard form letter (Dillman 2007). By nature, citizen scientists have a personal interest of self-education and a desire to contribute to science (Rotman et al. 2012); responding to a survey from a trusted source was an easy way to accomplish both goals and likely increased survey response.

Citizen Scientist Characteristics

Although no differences were detected between Disengaged and Engaged participant demographics, satisfaction with program, or landownership goals, which prohibited us from determining the characteristics that contributed to a reliable citizen scientist for the TQI project, we did find differences in knowledge gained from the program. This is particularly interesting when paired with the primary motivation and incentive to join the program reported by respondents, “To learn more about quail.” Seventy-one percent of respondents that left the program stated they did not gain knowledge in at least one quail related area (primarily quail management), compared to 47% of those that remained throughout the duration of the program (Figure 3). While the TQI had the goal and incentive, albeit secondary, of providing educational opportunities for citizen scientists (i.e., to learn more about quail), the project was designed and managed around the goal of conducting science with virtually no project design considerations for citizen scientists other than training them to collect and submit data. In general, citizen scientists were utilized as an economical data collection means. This is typical of citizen science projects and one of the main reasons they fail to reach their full potential (Rotman et al. 2012). In fact, scientists who have studied the efficacy of citizen-science projects have largely concluded that volunteer motivation must be factored into project design and that project typology or objectives should be clearly stated, *a priori*, in order to recruit and retain citizen scientists with similar goals (Jordan et al. 2011, Wiggins and Crowston 2011, Rotman et al. 2012, Nov et al. 2014). For example, Wiggins et al. (2011) surveyed the citizen-science literature and determined that most projects fall into 5 categories: Action, Conservation, Investigation, Virtual, and Education. These typologies are not absolute and projects often overlap categories; however, each project type required a different management style and projects were more successful in reaching intended goals when volunteer motives were matched to project typology (Jordan et al. 2011, Nov et al. 2014). Thus, citizen scientists that are seeking education should be recruited for and implemented into projects whose primary purpose is to increase awareness or educate volunteers. The TQI did not incorporate any volunteer motivations into project design other than the notion that collecting data on their land would result in more knowledge about quail management on their land. The project did not seek to connect those interested in science with more of the scientific portion nor did it entail any lessons learned or quail management modules specifically to participants. Rather, all volunteers were treated equally and tasked only with data collection and submission. This inadvertent failure to incorporate citizen scientists into project design could be one major factor contributing to the rapid decline of volunteer participation (Jordan et al. 2011, Nov et al. 2014).

In addition to potential project design problems, the TQI was time-consuming and labor-intensive compared to

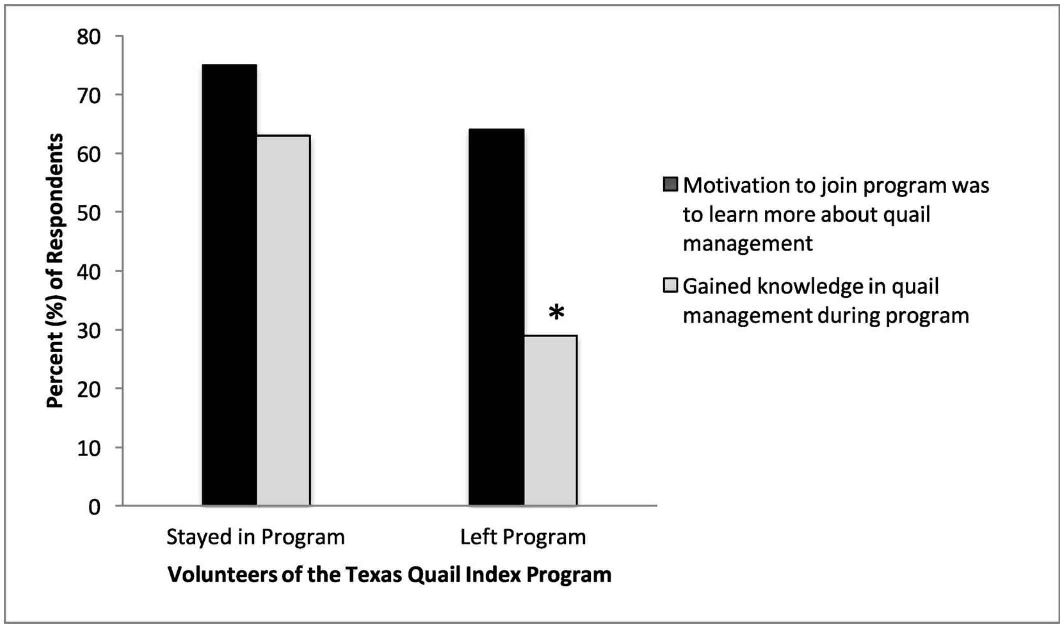

Fig. 3. Percentage of respondents to the Texas Quail Index Program post survey who joined the program to learn more about quail management (black) and who reported they gained knowledge in quail management during the program (grey). More respondents reported gaining knowledge in quail management during the program if they stayed in the program as compared to those that left early ($P = 0.021$). Statistical significance denoted by asterisk.

average citizen-science projects such as Project Feeder Watch (Cornell Lab of Ornithology 2007), the Christmas Bird Count (National Audubon Society 2007), or the North American Breeding Bird Survey (United States Geological Survey 2007). Most Disengaged participants (74.3%) reported they left the TQI because it was excessively time or labor intensive. Time required annually exceeded 60 hrs, not including travel to and from study sites (Reyna et al. 2012). The most collected variables of the TQI were the indices of relative abundance (call counts and roadside counts) which took about 4 hrs per outing and varied according to weather conditions and transect smoothness (i.e., for rougher transects, the volunteers had to drive slower). These indices of relative abundance are typical data to be recorded by volunteers in citizen-science programs. The least recorded variables of the TQI occurred in the 3rd quarter of each year, which entailed the most observable participation decline (Figures 1 and 2) and included the most laborious and time consuming data collection. Simulated-nest surveys (dummy nests) took ≥6 hrs to establish and approximately 8 hrs to check although the amount of time required checking the nests varied according to ease of finding them, which was often difficult. Predator scent-stations, forb species-richness, and habitat photos all required about 4 hrs to conduct and a moderate amount of labor (Reyna et al. 2012). Scent-stations were often rendered unusable because of precipitation and animal disturbance which some respondents considered frustrating and a waste of time (Reyna et al. 2012). These time estimates were for blocks of time, meaning all work within a task was done during one session; a large demand on a working adult's time. Although these laborious and time consuming tasks where not out of the question for payed technicians of a program, and volunteers were told about the time and tasks during training, it is easy to understand why the majority of Disengaged reported time and labor as the primary reason for leaving the program; it was too much work and this was not their primary job.

Further, the TQI lacked stipends and the only incentive to remain in the program was simply to learn more about quail (i.e., not monetized). This ulterior motive of the TQI may have been viewed as only a minimal enticement since nearly all citizen-science programs are designed to increase the scientific knowledge of the volunteer (McCaffery 2005). The TQI program did not reimburse volunteers for most project-related costs, including fuel for vehicles, photograph development, and supplies, so it is possible that the net benefit to some volunteers was perceived to be negligible. Most citizen-science projects lacking stipends are small-scale from the perspective of the volunteers and require very little labor and out-of-pocket expense. Most large-scale projects compensate volunteers for expenses and sometimes offer a stipend, resulting in increased productivity and likelihood of future service (Tschirhart et al. 2001).

Conclusions and Recommendations

The Texas Quail Index was a science-based project that utilized citizen scientists to collect data. The high rate of decline mimicked McCaffery's (2005) observation of participants being initially excited about collecting data and being involved in the scientific process, but later leaving the program. The TQI had a high rate of interest by volunteers but those interests (quail management education) did not line up with programmatic goals (quail science). Combined with an atypical amount of labor and time requirements, volunteer participation declined rapidly.

Debate will likely continue on whether or not citizen scientist data is reliable (Irwin 1995, McLaughlin and Hilts 1999, McCaffery 2005, Conrad and Hilchey 2011, Reyna et al. 2012) however, with technology continually making it easier to ensure data is collected properly (Yu et al. 2010, Kim et al. 2011), and with collaborative programs driving the future of citizen science along with technology (Sheppard and Terveen 2011), it is likely citizen scientist projects and programs will continue. Accordingly, we make the following recommendations as a result of our lessons learned. First, recruitment, project design, and management should incorporate the motives, interests, and typologies of volunteers. Rotman et al. (2012) found that volunteer motivation and interests changes during the duration of a project and that project managers should survey volunteers before the initiation of the project, and on a frequent basis thereafter, to better assign volunteers to tasks that align with their ever-changing motives. This further emphasizes the need to incorporate the motives of citizen scientists into project designs, or recruit volunteers whose typologies match programmatic goals. Ultimately, where these motivations are ignored volunteer participation declines (Jordan et al. 2011, Wiggins and Crowston 2011, Rotman et al. 2012, Nov et al. 2014). Second, citizen-science coordinators should keep volunteer tasks short and within the interest of the volunteer; long laborious projects are better left to payed employees. Most citizen scientists programs involve volunteers performing short tasks or collecting data in groups for one day or a series of well-planned short days (Cornell Lab of Ornithology 2007, National Audubon Society 2007, United States Geological Survey 2007). The TQI lost most of the volunteers due to time and labor intensiveness and as a result, data collection suffered (Reyna et al. 2012). Finally, our survey did not capture stipends or cost reimbursements contributing to the decline of volunteer participation but our review of the literature overwhelmingly emphasized that these factors play a big role in volunteer retention in long-term, large-scale projects, i.e., don't let the project be a cost to the volunteers but rather a benefit aligned with their motives.

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COMPARISON OF DOG SURVEYS AND FALL COVEY SURVEYS IN ESTIMATING FALL POPULATION TRENDS OF NORTHERN BOBWHITE

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ABSTRACT

The use of fall covey surveys to monitor population trends for northern bobwhite (*Colinus virginianus;* hereafter bobwhite) have been widely used in bobwhite research. Estimates of relative abundance from this monitoring technique are often important in assessing population responses to management practices or annual variation. However, conducting covey call surveys is labor intensive and typically can only be conducted during a narrow time frame. The use of dogs as a research tool may offer an efficient alternative to monitor bobwhite population trends. While dogs have been used in research for many other gallinaceous species, their application for bobwhite has received minimal research. To compare traditional and novel (dog) methods for both relative population abundance and density estimation, we conducted covey call surveys (50 points) and dog transects (32 km) during the fall (Sep-Oct) season from 2012-2014 at Beaver River WMA, Beaver County, Oklahoma, USA. A total of 306 detections were observed through fall covey count surveys, while only 44 detections were observed through dog transect surveys. Fall covey surveys yielded indices of 1.45, 2.04, and 3.21 detections per point count during 2012, 2013, and 2014, respectively. Dog transects yielded 0.23, 0.34, and 0.67 detections per km during 2012, 2013, and 2014, respectively. A Pearson's correlation coefficient of 0.996 indicated high correlation between indices estimated between both survey methods. However, the low sample size for detections during dog surveys precluded any analysis that would yield bobwhite density estimates. Our results indicate that dog transects can be a method for estimating abundance indices for bobwhite. However, if estimates of bobwhite densities are of interest, then use of dog transect surveys are not recommended as only under high quail densities or with high observer efforts do enough detections accumulate for robust density estimation unless large effort is expended.

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Key words: bird dogs, *Colinus virginianus*, covey surveys, population index, quail density, survey techniques

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THE EFFICACY OF GOPRO CAMERAS TO ACCOUNT FOR NORTHERN BOBWHITES FLUSHED, BUT UNDETECTED DURING AERIAL SURVEYS

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ABSTRACT

Estimating density and abundance is central to wildlife conservation for planning and decision-making purposes. Development of model-based techniques, such as distance sampling, allows researchers to estimate density with the inclusion of detection probabilities. However, the reliability of estimates obtained through this method are dependent upon the satisfaction of underlying assumptions, the most critical being that objects at zero distance from the observer be detected with 100% certainty. Conventional distance sampling, where line transects are traversed from an aerial platform, is a commonly used method to estimate northern bobwhite (*Colinus virginianus*) density over large, open areas. The restricted observer view from the helicopter raises concerns over undetected coveys flushing behind the helicopter. Our goal is to determine if GoPro cameras are a viable option to see coveys, if any, flushing behind the helicopter and thus, undetected by observers. We attached 2 GoPro Hero3+ cameras to a Robinson-44 helicopter while traversing line-transects during distance-sampling surveys in December 2015. Surveys were flown using 4 observers at an altitude of 10 m and a speed of 37 km/hour. Cameras were attached on either side of the helicopter to the door frame located between the front and backseats. We positioned GoPros facing down and toward the rear (tail) of the helicopter, a vantage point where observers may not be able to continually monitor. We set GoPros on video mode with a resolution of 960p and 60 frames per second. We will analyze the data by comparing video footage from the left and right side of the helicopter to time-stamped detection data. Preliminary analyses indicate that instances of coveys flushing behind the helicopter flight path are rare events. These data may be used to provide a correction factor to density estimates as well as provide us with insight into bobwhite response to helicopter activity.

Citation: Bruno, A., L. A. Brennan, A.N. Tri, and H. Su. 2017. The efficacy of GoPro cameras to account for northern bobwhites flushed, but undetected during aerial surveys. National Quail Symposium Proceedings 8:262.

Key words: *Colinus virginianus*, distance sampling, aerial survey, detection, GoPro

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DISTANCE SAMPLING TO ASSESS POST-GRAZING NORTHERN BOBWHITE RECOVERY IN SOUTH TEXAS

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) require habitat structure with substantial grass cover for nesting, predator avoidance, and thermal refuge. During the past 2 decades, many land managers have reduced or completely eliminated livestock across South Texas rangelands with the goal of improving bobwhite habitat. How bobwhites respond to post-grazing habitat recovery is unknown. Our objective is to investigate how bobwhites respond to the vegetative changes following removal of grazing. Our study is being conducted on a private ranch in Jim Hogg County, Texas and involves 3 different areas of post-grazing habitat recovery: a 1,246 ha area rested from grazing for 15 years; a 1,133 ha area rested 3 years from high grazing (7 ha/AU); and a 1,254 ha area rested 3 years from moderate grazing (14 ha/AU). Distance sampling surveys will be conducted on the 3 areas during December 2015 and 2016. Transects will be placed 400 m apart spanning all 3 study. Data collected during these surveys will be used to estimate bobwhite density on the 3 study areas and will be compared between sites and years. We hypothesize that the 15 years post-grazing area will have higher and more evenly distributed bobwhite density than the 3 years post-grazing at high intensity or medium intensity area.

Citation: Smith, R. A., L. A. Brennan, F. Hernández and H. L. Perotto-Baldivieso. 2017. Distance sampling to assess post-grazing northern bobwhite recovery in South Texas. National Quail Symposium Proceedings 8:263.

Key words: *Colinus virginianus,* distance sampling, northern bobwhite, post-grazing recovery, south Texas

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HUNTER-COVEY INTERACTIONS USING POINTING BIRD DOGS

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ABSTRACT

Hunting northern bobwhites (*Colinus virginianus*) with pointing dogs is a long-standing tradition in the Southeastern United States. Despite this rich hunting legacy, a paucity of empirical, behavioral information exists on the interaction between bobwhite coveys, pointing dogs and humans. As such, the efficiency of using pointing dogs to locate bobwhite coveys or an individual covey's behavioral response to hunting is poorly understood. During 2013 – 2015, we conducted hunts ($n = 192$) by mode of foot on Tall Timbers Research Station (TTRS, ~1,570 ha) in Leon County, Florida and horseback on a private property (2,023 ha) in Georgetown County, South Carolina. We captured bobwhites ($n = 741$) and fitted them with activity-switch enabled radio-transmitters, and we tracked coveys prior to, during and after hunts. We used 2 types of global positioning system (GPS) units to collect route data from dogs and hunters (via horseback or foot). We recorded encounter information (e.g., behavior, encounter type such as covey point or wild flush) in the field using a pre-configured application on an iPad and linked spatial data using a geographic information system (i.e., ArcGIS). On average, 52% of all radio-tagged coveys were available (within a dog's scent radius) during a hunt of which 73% were detected by pointing bird dogs. The overall probability of observing a covey on a hunt was 38% suggesting that most coveys within a hunting course go undetected. Vegetation density did not appear to be an impediment to bobwhite mobility or an important factor in detection of coveys by bird dogs. The potential reduction or manipulation of existing habitats may help to constrain where bobwhite coveys can escape to and covertly improve hunting efficiency. Furthermore, our results imply that a relatively high bobwhite density is required for sportsman to frequently encounter bobwhite coveys during a hunt.

Citation: Terhune II, T. M., D. J. McGrath, S. Wood and J. A. Martin. 2017. Hunter-covey interactions using pointing bird dogs. National Quail Symposium Proceedings 8:264.

Key words: bird dog, *Colinus virginianus,* covey, evasive behavior, hunting, northern bobwhite*,* radio-telemetry

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FACTORS INFLUENCING NORTHERN BOBWHITE HUNTER SUCCESS ON A PUBLIC WILDLIFE MANAGEMENT AREA IN KENTUCKY

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ABSTRACT

Hunter success is a critical measure of northern bobwhite (*Colinus virginianus*) restoration. Understanding the factors influencing hunter success can guide wildlife agencies in efforts to improve success and satisfaction and sustain hunter support of conservation initiatives. We compared use of vegetation types by radiomarked bobwhite ($n = 30$ coveys) and hunting dogs ($n = 241$) equipped with Global Positioning System collars during the 2014–2015 quail hunting season on Peabody Wildlife Management Area in western Kentucky. We surveyed hunting parties ($n = 252$) immediately after their hunt to determine success (flushed bobwhite) and gather hunt-party characteristics. We used associated habitat metrics from the dog track, weather variables, hunter and dog characteristics (e.g., age, experience), and hunt metrics (e.g., hours hunted, no. of dogs) to determine factors that influenced hunt success. Dogs used winter wheat firebreaks more than bobwhite regardless of time of day, forested areas more than bobwhite in the morning (0700–1000 hr) and midday (1000–1300 hr), disked areas more than bobwhite during midday, and open herbaceous areas less than bobwhite during morning and midday. The probability of success was positively influenced by number of dogs and hours hunted and negatively influenced by proportion of the hunt track in disked areas. Also, hunter success was greater in November compared with December and January. Our results indicated some key features associated with bobwhite habitat (open areas) may be underexploited by hunters, whereas other features (disked areas, firebreaks, and forested areas) may be overexploited. However, success was influenced primarily by factors that may be related to covey avoidance behavior resulting from substantial hunting pressure rather than where hunters selected to hunt. Lower bobwhite encounter rates (coveys flushed/hour) could cause hunter support to wane and bias hunting data as an indicator of population abundance.

Citation: Brooke, J. M., J. J. Morgan, D. L. Baxley, C. A. Harper, and P. D. Keyser. 2017. Factors influencing northern bobwhite hunter success on a public wildlife management area in Kentucky. National Quail Symposium Proceedings 8:265–272.

Key words: *Colinus virginianus,* hunter success, hunting, Kentucky, northern bobwhite

Sportsmen and women play an important role in the conservation of northern bobwhite (*Colinus virginianus;* henceforth, bobwhite) populations by contributing funding and support for land management (Brennan 2015). Understanding hunter success can have important implications for managing hunter satisfaction and harvest, and identifying factors related to hunter success and effort can help agencies manage bobwhite populations (Palmer et al. 2002, Tomeček et al. 2015). Bobwhite hunter success has been reported to be positively associated with bobwhite

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densities; therefore, success can be used as an inexpensive method to monitor bobwhite population trends (Palmer et al. 2002, Guthery and Mecozzi 2008).

Many factors besides bobwhite density can influence bobwhite hunter success including weather, landscape configuration, hunter and dog ability, and covey avoidance behavior (Michener et al. 2000, Wellendorf et al. 2012). Furthermore, comparing hunter and bobwhite use of vegetation types may further elucidate reasons for lower encounter or success rates (Richardson et al. 2008). By providing sportsmen with information regarding factors influencing success, agencies and managers may increase sportsmen success and satisfaction and therefore sustain future hunting efforts.

Considerable effort has been put forth by the Kentucky Department of Fish and Wildlife Resources to manage northern bobwhite populations on wildlife management areas open to public quail hunting. Monitoring efforts (fall-covey counts and spring-whistle counts) have indicated the population on Peabody Wildlife Management Area (WMA) has increased since 2009 at the onset of habitat management (Peters 2014, Morgan and Robinson 2015), but hunter success (coveys flushed/hour) has not followed the same trend (J. J. Morgan, unpublished data). Disparities in success and population estimates may be related to a multitude of factors but biologists and land managers within Kentucky's wildlife agency and at Peabody WMA have postulated that differences between bobwhite and hunters cover use resulting from hunting in an unfamiliar environment (reclaimed strip-mine vegetation), and covey avoidance behavior resulting from direct (bobwhite hunters) and indirect (rabbit hunters [Leporidae]) hunting pressure, may be the primary causes.

The objectives of our study were to 1) evaluate differences in vegetation types used by bobwhite and hunting dogs, and 2) evaluate the influence of hunt party, weather, and habitat characteristics on northern bobwhite hunter success on a public wildlife management area in west-central Kentucky to better understand the discrepancies between bobwhite populations monitoring efforts and hunter encounter rates.

STUDY AREA

We conducted our study on the Sinclair Unit (4,018 ha) of Peabody Wildlife Management Area (Peabody) in Muhlenberg County, Kentucky. Peabody is owned and managed by the Kentucky Department of Fish and Wildlife Resources and consists primarily of reclaimed strip-mine land. Open areas on Peabody were managed specifically for bobwhite; management practices included disking and herbicide application to control sericea lespedeza (*Lespedeza cuneata*). Disked open areas (open herbaceous or native warm-season grass) represented 1.9% of our study area and averaged 0.5 ha in size (Brooke et al. 2015). Firebreaks were 7–9 m wide and were disked and planted to winter wheat (*Triticum aestivum*) in August–September.

Forested areas comprised 51% of the study area and consisted of eastern cottonwood (*Populus deltoides*), green ash (*Fraxinus pennsylvanica*), and red maple (*Acer rubrum*) with an understory of brambles (*Rubus* spp.) and Japanese honeysuckle (*Lonicera japonica*). Open herbaceous areas dominated by sericea lespedeza, tall fescue (*Schedonorus arundinaceus*), field brome (*Bromus arvensis*), goldenrod (*Solidago* spp.), and common ragweed (*Ambrosia artemisiifolia*) comprised 20% of the study area. Areas dominated by shrubs and small trees (shrub cover), including black locust (*Robinia pseudoacacia*), sumac (*Rhus* spp.), autumn olive (*Elaeagnus umbellata*), and brambles, comprised 14% of the study area. Areas dominated by planted native warm-season grass comprised 1% of our study area. These 4 vegetation types made up 86% of our study area, with the remaining 14% in water (10%), firebreaks (2%), roads (1%), and developed areas (<1%).

METHODS

Field Methods

We captured bobwhite from August 2014 through December 2015 and radiotracked them from August 2014 through February 2015. We captured bobwhite using baited Stoddard (1931) funnel traps. We also used modified cast-nets at night to capture multiple individuals from radiomarked coveys (Truitt and Dailey 2000). We recorded sex, age, and body mass (g) of all captured individuals following protocols approved by the University of Tennessee Institutional Animal Care and Use Committee Permit 2042-0911. Individuals weighing >120 g were fitted with an approximately 6-g necklace-style very high frequency radiocollar (American Wildlife Enterprises, Monticello, FL, USA).

We tracked each covey ≥1 day/week throughout the hunting season (Nov–Feb). We monitored coveys throughout the day, obtaining 1 location/hour from 0700 hours to 1500 hours to determine daily temporal changes in bobwhite habitat use. We tracked each bird to ≥30 m and circled the bird to confirm the bird's location. We stayed ≥30 m from the covey to limit the observer biasing covey movements. We then recorded the Global Positioning System (GPS) location of the observer and azimuth and distance to the bird based on signal strength and direction and the vegetation type where the covey was located. Using the GPS location of the observer and the estimated azimuth and distance to the radio signal, we were able to determine the location of the covey. We assigned individuals to a covey based on their association with other radiomarked individuals. If a radiomarked individual was not located with its original covey on 3 consecutive days, we assigned that individual to a new covey. We used covey as the sampling unit rather than individual because locations from individuals within the same covey were not independent. We randomly selected one individual from each covey to represent the entire covey's location.

Quail hunting was permitted on Peabody Monday–Saturday, 0700 hours to 1500 hours. All hunting parties checked in and out at the WMA office and upon checking out parties were required to fill out a hunting log with information about their hunt party and hunt success. We collected the following information for each hunt party: group experience hunting quail (years), numbers of hours hunted, number of dogs used, coveys flushed, singles flushed, birds shot at, birds killed, and birds crippled. We also gathered information about dogs within each hunting party, including their age and experience hunting wild quail (years).

We acquired spatial data from hunting parties via Garmin Astro (Garmin Ltd., Olathe, KS, USA) collars attached to dogs within the hunting party to represent use of vegetation types by hunting parties. We asked hunters to voluntarily participate in our study upon arrival. We gave participants GPS collars to attach to hunting dogs used during the hunt, and set collars to record 1 location every 5 seconds. Units were returned upon the completion of the hunt and we downloaded data to the computer as text files. We manually checked each text file and identified and removed from the hunt track data the locations taken when the dog was not hunting (e.g., vehicle driving, at truck, in dog box). We gathered weather data for the day of each hunt from a weather station in the same county as our study site via Kentucky Mesonet (Western Kentucky University 2016).

Data Analysis

We estimated bobwhite habitat use by calculating the proportion of each covey's locations within each vegetation type. We also estimated the average distance from each vegetation type and access point for each covey. We defined access points (roads and firebreaks) as features that provided hunting parties easy access to potential hunting areas. For hunt parties, we estimated the length of the dog's hunt path in each vegetation type and divided it by the total path length, similar to Richardson et al. (2008). We also measured the average distance of locations on the hunt path to each vegetation type and access point. We were not able to attach collars to every dog in each hunt party. Therefore, for parties with multiple dogs, we randomly selected a track from one dog to represent the vegetation types used by the hunting party. We split the data into 3 time periods, morning (0700–1000 hr), midday (1000–1300 hr), and afternoon (1300–1500 hr) based on previously documented covey activity periods (Sisson and Stribling 2009, Crouch 2010) to capture temporal variation in bobwhite and hunter habitat use. We compared the proportions of quail locations and distance-to features with the proportions of dog hunt paths and distances-to features using 2-sample *t*-tests. We evaluated each variable for normality prior to analysis and transformed the data when appropriate (Shapiro and Wilk 1968). We used Mann–Whitney *U* nonparametric tests when normality could not be achieved with transformations (Kasuya 2001). The data reported are the untransformed means and confidence intervals. Significance for all tests was determined at an alpha of 0.05. For variables with significant relationships across time periods, we tested for significant differences in bobwhite and hunter cover use for each of the 3 time periods.

We determined the influence of hunt-party characteristics, weather, and habitat characteristics on hunt success (encountering ≥ 1 bobwhite) using binomial logistic regression. We used the glm function within the stats package of Program R (R package version 3.1.1, www.r-project.org, accessed 1 Dec 2015) to compare logistic regression models. We defined the dependent variable (hunt success) as flushing ≥ 1 bobwhite during the hunt (covey or single). We compared models using an Akaike Information Criterion (AIC_c) framework (Burnham and Anderson 2002). We first fit models using only weather, hunt, and hunt-party characteristics because we did not have habitat characteristic data for all hunts. Hunt and hunt-party variables included hours hunted, number of dogs used, group hunting experience (years), dog hunting experience (years), dog age (years) for all dogs used by the party, and the month the hunt occurred (categorical variable). Weather variables including maximum temperature, average wind speed, and total daily precipitation. Models included a null model (intercept only), single-variable models, models built based on experience hunting at Peabody, and a global model containing all variables. We used the top model from our first analysis as the base model for our habitat characteristic modeling exercise. We fit models containing habitat use variables using only hunting parties for which dog hunt tracks were recorded. We built models based on our habitat use data and data gathered previously on bobwhite selection from our study area (Brooke et al. 2015, Unger et al. 2015). We considered variables influential to hunt success if 95% confidence intervals for the beta estimate did not overlap zero.

RESULTS

We captured 251 individual bobwhite and tracked 30 coveys during the 2014–2015 quail hunting season, yielding 5,094 telemetry locations. We recorded hunt success information for 252 hunting parties, 143 of which also had associated dog track data. In total, we tracked 241 dogs from those 143 hunt parties, resulting in $>$500,000 locations. The average hunting party used 2.50 ± 1.74 (SD) dogs during the hunt and hunted 4.16 ± 1.38 hours. The maximum number of dogs used during a hunt was 12 dogs. Eight hours was the maximum amount of time hunted. The average dog covered 19.03 ± 8.57 km. Hunters harvested 222 birds, 31 of which were radiocollared, and 71.4% of hunt parties flushed ≥ 1 bobwhite. Hunting parties averaged encounter rates (coveys flushed/hour) of 0.25 ± 0.27 coveys/hour but averaged 0.58 ± 0.66 flushes/hour when including coveys and singles.

Dogs used areas farther from open herbaceous compared with coveys (Table 1). Furthermore, dogs used disked areas, firebreaks, and forested areas more than bobwhite coveys and open herbaceous and roads less than bobwhite coveys (Table 1). Throughout the day, dogs used firebreaks and forested areas 3.6 and 2.17 times more

Table 1. Mean cover type use by northern bobwhite covey and hunting dogs and associated 2-sample *t*-test results for cover types on Peabody Wildlife Management Area, Kentucky, USA, 2014–2015.

	Covey		Dog		*t*-test	
Variable	$\bar{x}$	95% CI	$\bar{x}$	95% CI	*t*-value	*P*-value[a]
Distance[b]						
Disked area	204.8	170.3–239.2	468.5	374.6–562.3	–2.00	0.05
Firebreak	115.1	92.7–148.4	223.2	163.2–283.3	–1.98	0.05
Forest	246.5	201.4–271.9	202.0	185.4–218.5	1.77	0.08
Native grasses	557.3	474.1–665.6	730.4	604.6–856.2	1.26	0.21
Open herbaceous	17.0	13.1–24.3	34.9	27.0–42.8	–3.30	$<$**0.01**
Road	130.6	106.4–144.9	188.0	174.5–201.4	–5.26	$<$**0.01**
Shrub	47.0	39.1–54.2	56.9	50.7–63.0	–1.71	0.09
Proportion[c]						
Disked area	3.2	1.5–4.8	6.6	5.6–7.5	0.36	$<$**0.01**
Firebreak	3.5	2.2–4.8	12.6	11.4–13.9	–7.49	$<$**0.01**
Forest	5.2	2.7–7.7	11.3	9.5–13.1	9,771[d]	$<$**0.01**
Native grasses	3.3	1.6–5.1	3.7	3.0–4.4	–0.71	0.71
Open herbaceous	54.9	48.8–61.0	42.8	40.4–45.3	3.68	$<$**0.01**
Road	3.4	1.9–4.9	0.7	0.5–0.8	11,302[d]	$<$**0.01**
Shrub	26.5	20.7–32.3	22.3	20.2–24.5	1.35	0.18

[a] Bold represents significant results at an alpha of 0.05.

[b] Distance (m) from bobwhite or dog location to each cover type.

[c] Proportion (%) of covey locations or proportion of dog track in each cover type.

[d] Represents Mann–Whitney *U* nonparametric test.

than bobwhite, respectively. Conversely, dogs used open herbaceous areas 1.28 times less than bobwhite. During the morning and midday, dogs used areas farther from open herbaceous compared with bobwhite (Table 2). Dogs used firebreaks more than bobwhite regardless of time of day, forested areas more than bobwhite during morning and midday, and disked areas more than bobwhite during midday (Table 2). Bobwhite used open herbaceous more than hunters during the morning and midday (Table 2). There were statistical differences in the distance from and use of roads by bobwhite and hunters; however, given the minimal use of roads by both hunters and bobwhite ($\leq$3% of locations), these differences are likely not biologically important.

Model ranking to determine factors related to bobwhite hunter success (Table 3) revealed time spent hunting, number of dogs used during the hunt, and month of the hunt influenced hunter success (Table 4). The addition of each dog to a hunt party resulted in a 6% increase in the probability of success compared with an 8% increase in success for each additional hour hunted (Fig. 1). Hunters were less likely to encounter a covey when hunting in December or January compared with hunting in November (Fig. 1). Although success was lower in February compared with November, the confidence intervals for the beta estimate overlapped zero, indicating success was indistinguishable between the 2 months (Table 4). Additionally, 4 habitat models explained variation in hunt success and included the proportion of disked area, shrub cover, and firebreaks in the hunt path (Table 3). The top model for habitat characteristics contained only disked area (β = –5.42, 95% CI = –10.6 to –0.36), suggesting amount of time a dog spent in disked areas had a negative relationship with success (Fig. 2). Shrub cover was included in 3 of the competing models and had a positive relationship (β = 2.13, 95% CI = –1.64–5.90) with success but the confidence intervals indicated the relationship was not significant. Conversely, firebreaks had a negative relationship (β = –2.81, 95% CI = –7.71–2.09) with success but the relationship was also not significant.

DISCUSSION

Use of vegetation types did differ between bobwhite coveys and hunters on our study area, indicating hunters may be overhunting certain vegetation types and underhunting others. However, these differences, with the exception of use of disked areas, did not influence hunter success; this suggests success is related to factors beyond hunter use of the landscape. Furthermore, the difference in use of features such as roads between coveys and hunters was minimal, suggesting a statistical significance but not a biological significance. Our results suggest factors related to mitigating covey evasion (a result of heavy hunting pressure), such as hunting early in the season, using multiple dogs, and hunting longer periods of time, were more predictive of success compared with habitat variables. Our results compliment the results of Orange et al. (2016), who reported hunters on our study area detected only 29% of available coveys. These results, coupled with those of Orange et al. (2016), provide insight into discrepancies between population estimates and hunter success. However, it should be noted that our study represents 1 year of data and subsequent years of data collection may result in differing conclusions. Nevertheless, these results can be used as a tool to

Table 2. Mean cover type use by northern bobwhite and hunting dogs by time period and associated 2-sample *t*-test results for significantly different ($P < 0.05$) cover types on Peabody Wildlife Management Area, Kentucky, USA, 2014–2015.

	Covey		Dog		*t*-test	
Variable	$\bar{x}$	95% CI	$\bar{x}$	95% CI	*t*-value	*P*-value[a]
Morning[b]						
Distance[c]						
Open herbaceous	16.3	9.0–23.7	26.8	13.5–40.2	−2.05	**0.04**
Road	125.0	90.1–159.9	165.9	132.8–199.1	−2.65	**0.01**
Proportion[d]						
Disk	4.3	1.0–7.7	5.7	3.5–7.8	−1.66	0.10
Firebreak	2.4	0.7–4.1	11.8	8.8–14.9	−7.65	<**0.01**
Forest	4.0	0.2–7.8	9.7	4.8–14.5	1,036[e]	<**0.01**
Open herbaceous	56.0	45.7–66.4	44.7	37.9–51.5	2.35	**0.02**
Road	4.0	0.8–7.1	0.7	0.3–1.0	1,205[e]	**0.04**
Midday						
Distance						
Open herbaceous	19.9	9.0–30.8	41.5	19.8–63.3	−2.40	**0.02**
Road	125.7	91.5–159.9	197.8	164.1–231.5	−3.74	<**0.01**
Proportion						
Disk	2.3	0.3–4.2	5.7	3.7–7.7	−3.50	<0.01
Firebreak	3.5	1.2–5.9	11.7	9.2–14.2	−6.27	<**0.01**
Forest	5.8	0.7–11.0	13.3	9.2–17.4	1,203[e]	<**0.01**
Open herbaceous	53.5	42.6–64.4	42.6	37.2–48.1	2.12	**0.04**
Road	3.4	0.6–6.1	0.7	0.4–1.0	1,508[e]	**0.01**
Afternoon						
Distance						
Open herbaceous	19.9	8.4–31.4	31.6	7.5–55.7	−1.17	0.24
Road	126.3	91.3–161.3	166.3	134.3–198.2	−2.38	**0.02**
Proportion						
Disk	2.9	0.1–6.0	4.3	2.4–6.2	−1.61	0.11
Firebreak	4.5	1.7–7.4	11.4	7.9–14.8	−3.72	<**0.01**
Forest	5.7	1.1–10.4	6.4	3.7–9.0	1,025[e]	0.06
Open herbaceous	55.2	43.5–66.8	46.3	40.3–52.3	1.67	0.10
Road	2.9	0.7–5.1	0.5	0.3–0.7	1,055[e]	0.10

[a] Bold represents significant results at an alpha of 0.05.

[b] Morning = 0700 to 1000 hr, Midday = 1000 to 1300 hr, Afternoon = 1300 to 1500 hr.

[c] Distance (m) from bobwhite or dog location to each cover type.

[d] Proportion (%) of covey locations or proportion of dog track in each cover type.

[e] Represents Mann–Whitney *U* nonparametric test.

educate bobwhite hunters using Peabody Wildlife Management Area.

Bobwhite use of the open herbaceous vegetation type exceeded 50% throughout the day whereas hunter use ranged from 42.6% to 46.3%. Although these unmanaged open areas were dominated by sericea lespedeza and were considered marginal for bobwhite (Brooke et al. 2015), the continuous cover likely served multiple purposes including roosting, feeding, and travel corridors between escape cover. Furthermore, open herbaceous areas included small patches of shrub cover that were too small to map as separate vegetation types but likely offered useable escape cover exploited by bobwhites throughout the day. Hunters likely used firebreaks more than bobwhite throughout the day because these linear features provided access to areas where hunters expected bobwhite to be located. However, these winter-wheat firebreaks did not provide adequate cover for bobwhite during the hunting season and were not selected by coveys (Brooke et al. 2015). Bobwhite use of forested areas was consistently low (<6% of locations) during the day, especially compared with availability of forested areas across our study area (51%), but hunter use of forested areas peaked during midday and was lowest during afternoon. The differences in hunter and bobwhite use of forested areas in morning and midday may be driven by hunters perceiving forested areas as escape cover for bobwhite.

Hunter use of disked areas more than they were used by bobwhite coveys and the associated negative relationship with success is surprising given the importance of these areas to bobwhite during the nonbreeding season on our study area (Brooke et al. 2015). Disking increased cover of food plants for bobwhite during winter (Brooke et al. 2015). Furthermore, Michener et al. (2000) reported both bobwhite and bobwhite hunters used fallow agricultural areas in Georgia similarly, which would be comparable to disked areas on our study area; and bobwhite encounters in Georgia were greater than would be expected in these areas. Temporal patterns indicated

Table 3. Logistic regression model selection results for northern bobwhite hunter success (encountering a covey) from Peabody Wildlife Management Area, Kentucky, USA, 2014–2015. Support for each model is indicated by the log likelihood (log(L)), corrected Akaike's Information Criterion values (AIC_c), the difference in corrected Akaike's Information Criterion values (ΔAIC_c), and Akaike model weights (w_i). All models contain an intercept.

Model	K	log(L)	AIC_c	ΔAIC_c	w_i
Hunt-party characteristics[a]					
hours + dogs + month	6	−137.11	286.6	0.00	0.74
hours + dogs + group exp.	4	−141.26	290.7	4.13	0.09
dogs + dog exp. + dog age	4	−142.11	292.4	5.83	0.04
dog exp.	2	−144.27	292.6	6.02	0.04
hours	2	−144.28	292.6	6.06	0.04
hours + dogs + dog exp. + max temp. + group exp. + precip. + wind + month + dog age	11	−135.42	293.9	7.38	0.02
dogs	2	−145.03	294.1	7.54	0.02
dog exp.+ group exp.	3	−144.26	294.6	8.07	0.01
max temp	2	−149.15	302.3	15.79	0.00
intercept only	1	−150.76	303.5	16.99	0.00
Habitat characteristics[b]					
hours + dogs + month + disk	7	−73.954	162.8	0.00	0.36
hours + dogs + month + disk + shrub	8	−73.074	163.3	0.50	0.17
hours + dogs + month + disk + shrub + firebreak	9	−72.431	164.3	1.52	0.15
hours + dogs + month + shrub	7	−74.826	164.5	1.74	0.12
hours + dogs + month	6	−76.154	165.0	2.17	0.09

[a] Hours = no. of hours hunted, dogs = no. of dogs used, month = month of hunt (categorical), group exp. = sum of group quail hunting experience (years), dog exp. = sum of dog experience hunting quail (years), dog age = sum of dogs used age (years), max temp. = maximum daily temperature, precip. = total daily precipitation, wind = average daily wind speed (mph).

[b] Disk = proportion hunt track in disked area, shrub = proportion of hunt track in shrub cover, firebreak = proportion of hunt track in firebreak.

hunters overexploited disked areas during midday. Bobwhite use of disked areas was 87% greater in morning compared with midday. Bobwhite may have shifted from feeding in disked areas in the morning to loafing in nearby cover during midday. Sisson and Stribling (2009) reported covey activity associated with feeding peaks 1–2 hours after sunrise and 1 hour before sunset.

It is plausible that variables most influencing hunt success on our study area (hours hunted, number of dogs used, and month of hunt) were related to the response of coveys to heavy hunting pressure. Radomski and Guthery (2000) suggested coveys were less likely to flush under heavy hunting pressure. Hunting pressure was not restricted on our study area and our study area also hosted one of the largest densities of rabbit hunters in the state (E. S. Williams, personal communication). Our finding of hunters being more successful in November compared with December and January strongly supports the notion that success decreased with repeated exposure of bobwhite coveys to hunting activity as the hunting season progressed. Orange et al. (2016) suggested hunters only flushed 29% of coveys on our study areas and 60% of coveys that had been missed were observed running from approaching dogs. Repeated contact with hunting dogs, both bird dogs and rabbit dogs, as the season progressed may further elicit this response and reduce the propensity of coveys to flush when encountered by a hunting party.

Table 4. Model beta estimates, confidence intervals, and odds ratios (exp(beta estimate)) for the most-supported model for northern bobwhite hunter success at Peabody Wildlife Management Area, Kentucky, USA, 2014–2015.

Variable	β-estimate	95% CI		Odds ratio
(Intercept)	−0.18	−1.29	0.83	0.93
No. of dogs	0.27	0.06	1.32	0.52
Hours hunted	0.32	0.10	1.38	0.56
Month[a]				
Dec	−1.00	−1.90	−0.17	0.37
Jan	−1.14	−2.03	−0.31	0.32
Feb	−0.79	−1.90	0.32	0.45

[a] Month is a categorical variable; therefore, each month must be compared with a reference month. The beta estimate for each month represents the probability of success compared with Nov (reference month).

Using multiple dogs during the course of a hunt could increase success for multiple reasons, such as allowing a hunt party to search a large area more thoroughly, be more effective in locating single birds from scattered coveys, and allow hunters to replace dogs as they become exhausted. Guthery and Mecozzi (2008) reported redundancy of hunted area (proportion of area in the hunt path searched by multiple dogs) was positively correlated with number of dogs used, suggesting using multiple dogs allowed hunters to more thoroughly search cover. Furthermore, multiple dogs may help mitigate covey avoidance behavior. Coveys were often observed running and scattering in the continuous open cover on our study when hunting dogs approached (J. M. Brooke, personal observation) and when a covey scatters it may reduce the ability of a single approaching dog to track the scent. Guthery and Mecozzi (2008) suggested the distance a hunting dog could detect bobwhite scent was reduced when dogs encountered single and pairs of bobwhite

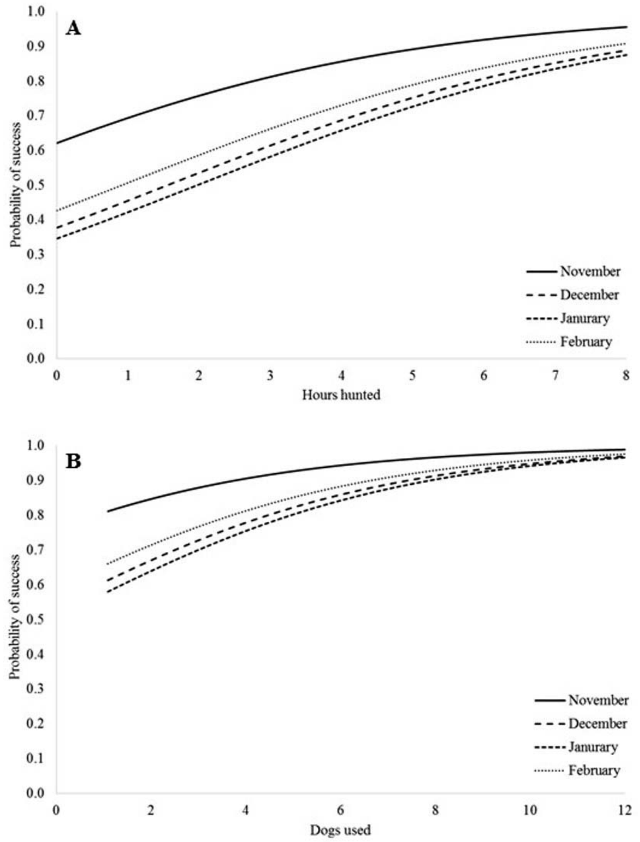

Fig. 1. Probability of success for northern bobwhite hunters on Peabody Wildlife Management Area, Kentucky, USA, 2014–2015. Success was influenced by hours hunted (A) and number of dogs used (B). Different line types represent differences in success based on the month in which hunting occurred.

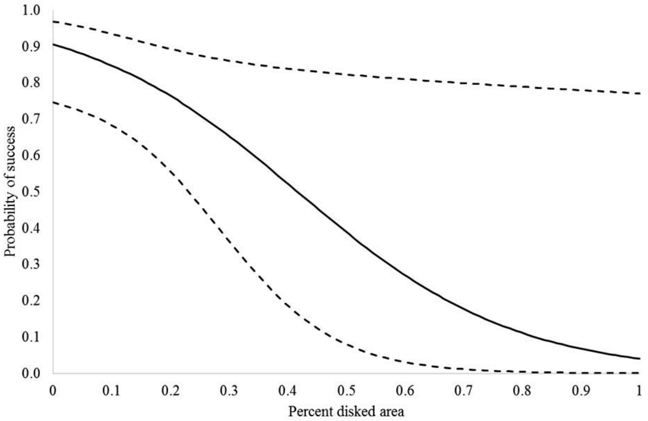

Fig. 2. Probability of success for northern bobwhite hunters based on the proportion of Global Positioning System hunt track within disked areas on Peabody Wildlife Management Area, Kentucky, USA, 2014–2015. Dashed lines represent the 95% confidence intervals around the probability of success.

compared with coveys. Therefore, using multiple dogs may have provided hunters with a larger scenting area to find individuals from scattered coveys or find coveys usually missed by a single dog.

Unsurprisingly, spending more hours afield increased the probability a hunting party flushing a bobwhite. However, given our encounter rate (0.25 coveys/hr), hunting parties may become discouraged and stop hunting prior to encountering a covey or be less likely to return in the future. Encounter rate is an important factor of hunter satisfaction (Richardson 2006) and low encounter rates may decrease hunter satisfaction and ultimately reduce the number of hunters pursuing bobwhite. Consistent hunting effort is an important consideration if hunter success is used as an index for bobwhite population monitoring. A considerable reduction in hunter effort may preclude use of this index (Palmer et al. 2002). Educating hunters on factors influencing success may be vital to maintain or increase hunter satisfaction and encourage future participation.

One issue hunters raised throughout our project was concern regarding the influence of repeated contact between research technicians and coveys and the potential impact on covey behavior. Technicians did track coveys throughout the day, but flushed the covey on $<1\%$ of tracking events (J. M. Brooke, unpublished data). Perkins et al. (2014) suggested bobwhite flew shorter distances, at slower speeds, and landed in areas with less visual obstruction when flushed by researchers compared with when flushed by hunters or raptors. This suggests bobwhite do not perceive the threat posed by researchers similarly to other threats. Furthermore, our fall covey counts on Peabody suggested there were ≥ 77 coveys on our area but we only radiomarked 30 coveys, indicating more than half of the coveys on our study area may have not had any contact with researchers (E. S. Williams, unpublished data). Therefore, we conclude that researchers had minimal if any effect on covey behavior on our study area.

MANAGEMENT IMPLICATIONS

Our results suggest focusing hunting efforts on disked areas, especially during midday (1000–1300 hr), may decrease hunter success. Therefore, we suggest hunter effort should be focused on cover around disked areas (shrub and open herbaceous), outside of peak feeding times (1–2 hr after sunrise). Furthermore, hunters should avoid venturing into forested cover away from open areas. Factors such as covey-avoidance behavior may strongly influence bobwhite encounters, especially when hunting pressure is unrestricted; and our results suggest using multiple dogs during the hunt, hunting longer periods, and hunting early in the season increase success. Managers may consider reducing hunting pressure in an effort to increase hunter success throughout the hunting season. However, it is important to consider that nonbobwhite hunting on public areas, such as rabbit hunting, also may contribute to unintentional hunting pressure on bobwhite. Our results can be used to educate hunters about factors influencing hunter success and may help sustain future hunter participation, which may have direct implications for future funding or population monitoring efforts.

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EVALUATING HUNTING SUCCESS OF PEN-REARED AND WILD NORTHERN BOBWHITE IN A RECLAIMED KENTUCKY MINELAND

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ABSTRACT

Northern bobwhites (*Colinus virginianus*) have experienced severe population declines across their distribution. In order to address population declines and to continue providing hunting opportunities, multistate efforts have been undertaken to stabilize and restore bobwhite populations. Ongoing efforts using the National Bobwhite Conservation Initiative's quail focus area approach have so far demonstrated success throughout Kentucky. However, population increases in the Peabody Bobwhite Focal Area, in western Kentucky, have not been correlated to increases in perceived hunter success. Consequently, some sportsmen question the effectiveness of focal area conservation. In response to hunter concerns, we tested dog hunting ability with wild and pen-reared bobwhites. We also measured evasive behaviors of wild bobwhite using radiotelemetry. During the 2013–2014 and 2014–2015 hunting seasons we conducted 114 dog trials. Dogs detected bobwhite during 46 of 59 (78.0%) pen-reared trials and 16 of 55 (29.1%) wild bird trials. When dogs did not detect wild quail, birds ran away 64.1% of the time and remained motionless 20.5% of the time. Using an information-theoretic approach, we determined that bird type (wild vs. pen-reared) had a significant effect on bird detection, with dogs 8.62 times more likely to detect pen-reared birds than wild birds. We recommend that hunters be informed about differences in dog detection rates between pen-reared and wild bobwhite so that public support needed for wild bobwhite restoration can persist.

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Key words: *Colinus virginianus,* dog trial, hunter success, Kentucky, northern bobwhite, pen-reared

As a response to long-term and persistent population declines, more emphasis is being placed on northern bobwhite (*Colinus virginianus;* hereafter, bobwhite) conservation now than at any point in history. Currently, state-wide efforts are underway to restore and enhance vegetation communities that support bobwhite populations, and these conservation efforts have led to site-specific population increases throughout Kentucky (Peters 2014, McKenzie et al. 2015, Morgan and Robinson 2015). However, sportspeople are one of the key catalysts to fund and champion expensive habitat enhancements (Brennan 2015). Scientific monitoring programs may demonstrate successes through increased population abundance; however, if hunters do not experience enhanced hunting success, public support for conservation activities may be fleeting.

Although most studies report a positive correlation between hunter success (coveys flushed per hour) and quail population densities (Smith and Gallizioli 1965, Brown et al. 1978, Palmer et al. 2002, Mecozzi and Guthery 2008, Stribling and Sisson 2009), this trend has not been observed on some Kentucky state-managed lands. For example, within Peabody Wildlife Management Area (PWMA), the bobwhite population has roughly doubled between 2009 and 2013 (Morgan and Robinson 2015); however, perceived hunter success and satisfaction

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has not markedly increased. This has led some sportspeople to question the success of management activities. Although little is known about this phenomenon, a number of suppositions have been presented by resource professionals to explain why perceived hunter success has not increased as a response to increased bobwhite densities on PWMA.

The dramatic reduction of wild bobwhite over the past 50 years (Sauer et al. 2014) has fostered a culture of releasing pen-reared bobwhite to satisfy hunter demands while preserving the tradition of hunting (Kozicky 1993, Schulz et al. 2003). A similar paradigm has long existed for sport fishing. Based upon a survey of Kentucky bobwhite hunters, 33% of respondents reported to have hunted pen-reared quail in the 2008–2009 hunting season (Responsive Management 2009). Behavioral differences have been observed between pen-reared and wild quail (Roseberry et al. 1987, Perez et al. 2002, Jung 2010); therefore, hunting pen-reared quail may lead to a decline in both dog and hunter ability to hunt for wild quail. For example, compared with wild quail, pen-reared bobwhites have been observed to be more reluctant to flush when approached (Klimstra 1975, Roseberry et al. 1987) and fly slower and flush shorter distances following disturbance (Perez et al. 2002). Additionally, although wild birds forage in close proximity to escape cover (Brooke et al. 2015, Unger et al. 2015), pen-reared quail forage in areas with less concealing cover (Roseberry et al. 1987), where they may more exposed to hunting parties.

Furthermore, the high hunter success that commonly results from hunting pen-reared birds may alter hunter perceptions regarding harvest expectations. As pen-reared quail are considered to be easier to hunt than wild quail, hunters may become frustrated with low rates of covey detection observed in some wild populations. The coupling of elevated hunter expectations for harvest and limited ability to detect wild birds could be problematic for maintaining support for wild bobwhite restoration efforts.

To fully understand harvest rates, it is important to understand the factors that drive bobwhite detections while hunting. Although research exists on the factors that may influence wild game-bird detection and harvest success (Sisson et al. 2000, Palmer et al. 2002, Asmyhr et al. 2012, Wellendorf et al. 2012), little research exists regarding detection differences between wild and pen-reared birds. Therefore, we designed an experiment with the primary objective to model factors that explain a bird dog's ability to hunt for bobwhite. Specifically, we investigated detection differences between wild and pen-reared bobwhites.

STUDY AREA

This study was conducted at Peabody Wildlife Management Area (PWMA) located in Muhlenberg and Ohio counties in western Kentucky. This reclaimed coal mine site is 3,323 ha in size and is managed by the Kentucky Department of Fish and Wildlife Resources. PWMA is a quail focus area in Kentucky's bobwhite restoration plan (Morgan and Robinson 2008). Primary vegetation types within the study area have been characterized by Brooke et al. (2015) and they include open herbaceous (36%), mixed-shrub (25%), native warm-season grass plantings (8%), forested woodland (22%), and other (9%). Extensive coverage of sericea lespedeza (*Lespedeza cuneata*) occurs throughout PWMA.

METHODS

Dog trials

To identify research participants, we solicited an application for volunteer dog handlers (limited to 2 dogs/handler) through quail grassroots organizations (e.g., Quail Forever, St. Paul, MN, USA), social media (e.g., Facebook; Facebook, Inc., Menlo Park, CA, USA), and known hunters at PWMA. We screened applications to reduce variability by selecting those that had dogs that were 3–8 years of age and had hunted or participated in field trials ≥5 times/year. We categorized bird dogs into 2 groups: those with little-to-no exposure (≤25% of bird/dog encounters) to pen-reared birds (hereafter, wild dogs), and those with high-to-exclusive exposure (≥75% of bird/dog encounters) to pen-reared birds (hereafter, liberated dogs).

We conducted this study during the 2013–2014 and 2014–2015 bobwhite hunting seasons. During each hunting season we conducted 4 dog trials, with 2 trials conducted early in the hunting season (Oct and Nov) and 2 late in the hunting season (Dec and Jan). There were 4 wild dogs and 4 liberated dogs at each trial date. Each trial required 8 radiomarked wild coveys and 8 pen-reared coveys because we exposed dogs to 1 wild and 1 liberated covey. All wild birds were captured and fitted with radiotransmitters as part of a collaborative research project investigating bobwhite survival and habitat use (Brooke et al. 2015, Peters et al. 2015). As part of this collaborative research, individuals were tracked 3 days/week using radiotelemetry, and birds were assigned to coveys based upon their repeated proximity with other radiotagged birds. Between 2 and 6 radiotagged bobwhite were present within each wild covey. We conducted dog trials on wild individuals more than once, but we limited repetition to 1 early and 1 late season trial per wild covey. During the site selection process for the pen-reared trial, we made efforts to ensure vegetation parameters were consistent between wild and pen-reared trial locations by choosing sites in which wild radiotagged bobwhite were commonly located during companion bobwhite research. Capture, handling, and telemetry protocols of wild birds complied with the University of Tennessee Institutional Animal Care and Use Committee (Permit 2042-0911). Animal care and use protocols for this study were reviewed and approved by the Kentucky Department of Fish and Wildlife Resources.

Dog trials began at approximately 0800 hours at each site (wild and pen-reared sites). Trial teams consisted of a team leader, dog, dog handler, and extra assistants to assist in flushing undetected coveys. Additionally, a radiotelemetry technician was present during wild bobwhite trials. At wild covey trial locations, the telemetry technician located radiotagged individuals within coveys from a distance of ≥50 m. The technician, team leader, handler, and leashed dog approached the covey to approximately 100 m downwind. A hunt bearing was established by the telemetry technician. The team leader formally began the trial by directing the handler to keep the dog within the hunting corridor (100 m on either side of the hunt bearing). The dog was unleashed along the hunt bearing and the team leader followed the dog closely noting dog behavior. Dog handlers were instructed to hunt as they would normally, including use of bells, beepers, and whistles. Technicians and team leaders were discrete in use of telemetry and dog handlers were not aware of covey locations. The Global Positioning System (GPS) coordinates of trial start locations were recorded prior to unleashing bird dogs.

During wild bird trials, the telemetry technician constantly monitored radiotagged individuals within coveys to evaluate bobwhite evasive behaviors. When dogs did not detect wild quail, the telemetry technician determined whether the majority of radiotagged birds within the covey either ran away or remained motionless when the dog passed the covey location. Telemetry technicians were highly experienced with tracking bobwhites in the study site because they had been working within this area for 2–3 months prior to trial dates. Any dog point was followed by an attempted handler flush with results noted. We defined a dog point as the action in which a dog stopped, remained motionless, and aimed its muzzle at a potential bobwhite location. An individual bobwhite or covey flush at any time ended the trial. We defined detection as a covey or individual flush by the dog, point followed by an individual or covey flush by the handler, or a point followed by an individual or covey flush by the dog. If the handler and dog passed the covey by ≥100 m, the radiotelemetry technician stopped the group.

We conducted trials of pen-reared birds in the same fashion with the exception of the lack of radiotelemetry. We acquired all pen-reared bobwhites from suppliers that raised birds in flight conditioning pens. We soft-released pen-reared birds (Fies et al. 2000) in groups of 8–10, approximately 1–4 hours prior to dog trials. During release, field staff placed the boxed birds on the ground. Field staff uncovered a precut hole in the side of the box and then quietly vacated the area. For pen-reared bird trials, teams approached the soft-release locations to approximately 100 m downwind, at which point they established a hunt bearing and began trials.

If dogs did not detect wild or pen-reared bobwhite on the first pass, teams were rerouted to a corridor perpendicular to the covey as a second opportunity to detect birds. Upon completion of the first trial, the groups reconvened and switched trials. For example, a group starting with wild birds switched to pen-reared birds. The second dog trials began at approximately 1030 hours. Teams stopped a dog trial and we censored it from analysis if wild or pen-reared bobwhite were flushed by the trial team (handler or technicians), independently of detection by the dog.

Immediately following the completion of both wild and pen-reared dog trials, field researchers asked dog handlers to independently complete a hunter survey regarding their experiences. Questions within the survey included 1) what best represents your perspective on wild bobwhite covey behavior during the trial, and 2) what best represents your perspective on liberated bobwhite covey behavior during the trials? There were 4 response choices: 1) as expected, 2) more evasive, 3) less evasive, or 4) no opinion.

Weather Data

Quality Controlled Local Climatological Data were obtained from a National Oceanic and Atmospheric Administration automated weather station located at Madisonville Regional Airport (Madisonville, KY, USA), which was approximately 35 km from the study site. Weather data at this station were recorded at 20-minute intervals. Weather data variables included ambient temperature (°C), barometric pressure (in.Hg), relative humidity (% RH), and wind speed (m/sec). To obtain time specific weather data, we used weather values that were closest to the starting time of the trial. When the trial started between 2 weather recording intervals, we averaged the 2 relevant weather values.

Vegetation Sampling

Following dog trials, we recorded key vegetation components that may influence a bird dog's ability to detect scent within hunt corridors (200-m × 200-m area bifurcated by the hunt azimuth). We conducted vegetation surveys between 4 and 6 weeks after dog trial dates. We completed vegetation surveys for the early season trials in December and January prior to the start of late-season trials. We completed vegetation surveys for late-season trials in March and early April, prior to the growing season.

We used GPS coordinates recorded at the onset of trials, prior to unleashing bird dogs, as the starting point for vegetation sampling transects. We recorded vegetation data along the original hunt corridor at 4 distance intervals (50 m, 100 m, 150 m, and 200 m). We measured vertical plant structure using a Nudd's Vegetation Profile Board (Nudds 1977). We quantified visual obstruction using a 2-m-tall and 25-cm-wide profile board, consisting of 8, 25 × 25-cm, alternating black and white intervals (Nudds 1977). We recorded the proportion of vegetation covering each interval at a distance of 10 m and a height of 1.5 m from the east and west sides of the transect. We averaged the 8 visual Nudd's board readings per trial corridor to create a single value per strata for each dog trial location.

We measured openness at ground level using a sight tube (Gruchy and Harper 2014). We mounted a polyvinyl chloride pipe (3.8 cm diam, 15.2 cm long) on a stake 15.2 cm above ground. We held a brightly colored plastic ruler (30.48 cm) in front of the tube opening and moved it away until ≥75% of the ruler was obscured by vegetation. We

Table 1. Nudd's visual obstruction profiles (±SE), percent coverage of primary vegetation types, and sight tube readings at trial locations of dogs' ability to detect wild ($n = 55$) and pen-reared ($n = 59$) northern bobwhite during 2013–2015 at Peabody Wildlife Management Area, Kentucky, USA[a]. Results of 2-sample *t*-tests (*P*-values) comparing pen-reared and wild bird trial locations are reported.

Trial group	Nudds4	Nudds6	Nudds8	Native	Nonnative	Grass	Forbs	Woody	Sight tube
Pen-reared									
Mean	20.00	52.93	82.84	20.47	79.53	33.90	63.47	25.00	2.55
SE	2.23	3.71	2.14	1.68	1.68	2.44	2.18	2.00	0.13
Wild									
Mean	21.71	54.13	83.24	23.64	76.36	33.18	54.73	23.05	2.61
SE	2.13	2.84	2.05	2.46	2.46	2.81	2.87	2.62	0.13
t	−0.55	−0.25	−0.13	−1.07	1.07	0.19	2.45	0.59	−0.33
P (2-tailed)	0.583	0.800	0.894	0.285	0.285	0.847	0.016	0.553	0.740

[a] Nudds8: percent vegetation cover at stratum 8; Nudds6: percent vegetation cover at stratum 6; Nudds4: percent vegetation cover at stratum 4; RH: relative humidity; Sight tube: average sight tube value of trial corridors.

measured and recorded the distance from the midpoint of the tube to the ruler. If the ruler was visible at 5 m distance, we considered this a maximum value. We collected data at each of 4 distance intervals (50 m, 100 m, 150 m, and 200 m). We collected sight tube readings 5 m to the east side of the transect to prevent vegetation trampling. We recorded the first reading by sampling perpendicularly from the transect. Observers then moved 1 m forward and collected the second sight tube reading. We averaged sight tube readings to create a single value for each trial location. Finally, we evaluated the entire hunt corridor to obtain an overall visual estimate of species composition. First we evaluated the hunt corridor to determine the percent coverage of native versus nonnative vegetation (i.e., sericea lespedeza). Then we evaluated the hunt corridor to determine the percent coverage of 3 functional vegetation types: grass, forbs, and woody cover.

We averaged vegetation cover (native vegetation, nonnative vegetation, grass, forbs, and woody cover), sight tube, and Nudd's board readings across wild and pen-reared trial locations and compared them using a 2-sample *t*-test. We designated a *P*-value of 0.05 and, following Bonferroni correction, considered tests significant at $P < 0.004$.

Logistic Regression

Our response was binary (detection or no detection) and we had several predictive variables, so we used multiple logistic regression analysis with *a priori* model selection to predict the influence of our variables on a dog's ability to detect birds. Before analysis we used a Pearson's correlation matrix to detect highly correlated predictive variables ($|r| > 0.70$). Several variables were highly correlated with other predictive variables and were therefore removed, including dew point and Nudd's board readings at strata 1, 2, 3, 5, and 7. Nudd's board strata 4, 6, and 8 essentially represent distinct classes of vertical vegetation structure: low, mid, and high.

We used second-order Akaike's Information Criterion (AIC_c) as a method of model selection (Burnham and Anderson 2002). We developed 18 biologically relevant models using weather variables, trial specifics, vegetation measurements, and dog details. Logistic regression and model selection were performed using the package 'glm' and 'AICcmodavg' (Mazerolle 2012) in Program R (R Version 3.2.2, www.r-project.org, accessed 11 Nov 2015; R Core Team 2015). Modeled variables included bird type (pen-reared vs. wild), hunting season (2013–2014 or 2014–2015), wind speed (m/sec), time of day, sight tube readings, barometric pressure (in. Hg), ambient temperature (° C), season timing (early vs. late), Nudd's board measurements (intervals 4, 6, and 8), dog experience classification (wild vs. liberated), and percent relative humidity (RH). We did not perform multimodel inference because the top model had AIC_c weight close to 1.0. We assessed statistical significance of model coefficients using 85% confidence intervals (Arnold 2010) with results excluding zero considered statistically significant.

RESULTS

We conducted 114 dog trials during the 2013–2014 ($n = 53$) and 2014–2015 ($n = 61$) bobwhite hunting seasons. Of these 114 trails, 55 were conducted with wild birds and 59 with pen-reared birds. Following Bonferroni correction, vegetation measurements were similar between wild and pen-reared dog trial locations (Table 1). Dogs detected bobwhite during 46 of 59 (78.0%) pen-reared trials and 16 of 55 (29.1%) wild bird trials. During wild bird trials, liberated dogs detected bobwhite in 8 of 24 (33.3%) trials and wild dogs detected bobwhite in 8 of 31 (25.8%) trials. During pen-reared bird trials, liberated dogs detected bobwhite in 22 of 27 (81.5%) trials and wild dogs detected bobwhite in 24 of 32 (75.0%) trials. When dogs did not detect wild quail, we observed birds running away 64.1% of the time and remaining motionless 20.5% of the time. We were unable to confidently identify wild bird responses during 15% of unsuccessful trials. Although we did not statistically analyze the second pass of each trial, we conducted second passes during 44 trials (9 pen-reared and 35 wild), of which dogs detected bobwhite in 55.6% of pen-reared and 22.9% of wild bird second attempts.

Following dog trials, 52 dog handlers participated in posttrial surveys, representing 91.5% of the total trials conducted. When asked what best represents their perspective on wild bobwhite behavior during the trial:

Table 2. Selection for candidate models, from logistical regression, to explain northern bobwhite detection by hunters using dogs at Peabody Wildlife Management Area, Kentucky, USA, 2013–2015.

Model	K^a	$AIC_c{}^a$	$\Delta AIC_c{}^a$	$w_i{}^a$
Bird type (pen-reared vs. wild)	2	132.66	0.00	1
Global	15	153.55	20.89	0
Wind speed	2	159.05	26.39	0
Intercept only	1	159.19	26.54	0
Year	2	160.59	27.93	0
Time of day	2	160.94	28.28	0
Barometric pressure	2	161.07	28.41	0
Ambient temperature + Wind speed	3	161.12	28.46	0
Sight tube	2	161.16	28.50	0
Ambient temperature	2	161.25	28.59	0
Season timing (early vs. late)	2	161.26	28.60	0
Nudds8	2	161.26	28.60	0
Nudds6	2	161.27	28.61	0
Nudds4	2	161.27	28.61	0
Dog experience (liberated vs. wild)	3	161.46	28.80	0
Ambient temperature + Sight tube	3	163.27	30.61	0
Ambient temperature + RH	3	163.32	30.66	0
Ambient temperature + RH + Wind speed + Sight tube	5	165.41	32.75	0

[a] Abbreviations: AIC_c: Akaike's information criterion adjusted for small sample sizes; K: no. of parameters; ΔAIC_c: difference between AIC_c of best fitting and current model; w_i: Akaike's weight; Nudds8: percent vegetation cover at stratum 8; Nudds6: percent vegetation cover at stratum 6; Nudds4: percent vegetation cover at stratum 4; RH: relative humidity; Sight tube: average sight tube reading at trial corridor.

38.5% of participants indicated that they behaved as expected, 57.7% of participants indicated that they were more evasive than expected, 0% of participants indicated they were less evasive than expected, and 3.9% of participants indicated that they had no opinion. When asked what best represented their perspective on pen-reared bobwhite behavior during the trials: 69.2% of participants indicated that bobwhite behaved as expected, 17.3% of participants indicated that bobwhite were more evasive than expected, 9.6% of participants indicated bobwhite were less evasive than expected, and 3.9% of participants indicated that they had no opinion.

Model selection indicated that the most parsimonious model included bird type (wild vs. pen-reared; $AIC_c = 132.66$; $w_i = 1.00$; Table 2). Estimated odds of a dog detecting a pen-reared bird were 8.62 times higher than the odds of a dog detecting a wild bird (4.70–16.35 85% CI, $\beta_{wild} = -2.15 \pm 0.43$ SE). We did not observe a significant relationship in any other variables included in our analysis based on β estimates, because 85% confidence intervals overlapped 0.

DISCUSSION

The results of our study indicated that bird detection was influenced primarily by bird type (wild vs. pen-reared). Based upon odds-ratios, dogs were 8.62 times more likely to detect pen-reared versus wild birds. With the exception of bird type, little association was observed between bird detection and other variables included within our AIC_c models.

Observed differences in detection were likely a result of behavioral or scent emission dissimilarities between pen-reared and wild birds. For example, numerous behavioral differences have been observed between wild and liberated pen-reared bobwhites (Klimstra 1975, Roseberry et al. 1987, Perez et al. 2002, Jung 2010), which may make liberated birds easier to detect. Additionally, scent emission differences between wild and pen-reared birds may have facilitated differences in detection. For instance, pen-reared birds may be more readily detected by dogs because they were temporarily held in soft-release boxes where they were likely exposed to fecal matter increasing scent emission. Behavior and scent emission dissimilarities were likely 2 of the key factors that caused differences in detection between pen-reared and wild bobwhite.

We did not observe an association between dog experience classification (wild vs. liberated) and bird detection. Although not statistically significant, liberated dogs, with greater experience hunting pen-reared birds, were marginally more likely to detect wild coveys than were wild dogs with greater experience hunting wild birds. The similarity in detection rates between wild and liberated dogs is contrary to expectations. Based upon posttrial survey results, 68.6% of participants indicated that they expected liberated dogs to find wild coveys at a lower rate. However, our results do not support this contention. Repeated exposure to pen-reared quail does not appear to decrease the effectiveness of bird dogs when hunting wild quail. It is possible that liberated dogs may have more overall hunting experience (i.e., days in the field) than wild dogs, which may facilitate increased bird detection; however, this is an area that warrants future research.

Although we included a seasonal variable (early vs. late season) in our model, timing of trials did not have an influence on bird detection. Similarly, in Florida and Georgia (Palmer et al. 2002, Wellendorf et al. 2012), time of season was not shown to significantly impact bobwhite hunting success. On our study site, it is likely that either birds uniformly exhibit avoidance behavior throughout the season as a result of high hunt intensity, particularly rabbit (Leporidae) hunting pressure, or our sample sizes may have been too small to detect significant effects of seasonality on bobwhite detection.

Within our study there were a number of research limitations. Although pen-reared quail had no covey affiliation prior to soft-release, we observed birds behaving as a covey following release. Bobwhites are gregarious, so it is unlikely that pen-reared birds separated following soft-release; however, we recognize this possibility as a limitation of our study design. In an effort to prevent pen-reared birds from scattering from the release site, we limited the time between soft-release and the beginning of trials. Our high pen-reared detection rates validate that liberated birds remained in the hunting corridor during trials. We recognize that the scent characteristics of soft-release boxes may have facilitated detection of pen-reared bobwhite by dogs; however, we made efforts throughout the study to limit time that coveys were contained within soft-release boxes. Finally, few weather and vegetation variables appeared to influence bird detection. This may be a result of small samples sizes because our study was logistically limited in the number of dates it was conducted. Future research should be conducted to investigate the impact that environmental, especially weather, variables may have on bird detection.

Although we did not directly investigate the factors that influence hunter satisfaction, we postulate that hunting pen-reared quail may have unexpected consequences on hunter perceptions. Many quail hunters in Kentucky hunt pen-reared bobwhite and it is possible that hunter perceptions may influence hunter satisfaction. For example, during participant surveys, most hunters reported that wild coveys were more evasive than expected. The relatively lower detection rates experienced when hunting wild bobwhite, as compared with pen-reared bobwhite, may reduce hunting satisfaction when pursuing wild birds. However, hunters may increase detection rates by thoroughly searching an area repeatedly following a false point because, as our results show, it is likely that wild coveys are remaining motionless or running away when dogs pass a covey location. As our results have demonstrated, a second pass through an area suspected to contain wild birds may be an effective way to increase hunting success. Furthermore, hunters may benefit from using more than 1 dog during hunting trips because research has shown that exploration rates and hunt corridor size increases as the number of dogs within parties increases (Guthery and Mecozzi 2008).

MANAGEMENT IMPLICATIONS

Bird type has the potential to significantly affect detection, with dogs 8.62 times more likely to detect pen-reared birds than wild birds. With a significant proportion of Kentucky bobwhite hunters harvesting pen-reared quail, high detection rates experienced when hunting pen-reared birds may reduce hunting satisfaction with the relatively lower detection rates experienced with wild bobwhite. We suggest that land managers work to educate hunters regarding detection differences between wild and pen-reared birds. Future research is needed to evaluate hunter satisfaction in the context of wild and pen-reared bobwhite.

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REFINING THE HUNTING ZONE OF HUNTER-COVEY INTERFACE MODELS

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ABSTRACT

Regulating harvest is important to sustain northern bobwhite (*Colinus virginianus*) populations. Direct measures to control harvest such as setting fixed proportions (i.e., percent of fall population) are not typically feasible, thus, indirect measures (e.g., managing access, season length) are more commonly used. However, these measures are predicated on relationships between hunter effort and kill rate (K) which is a function of several parameters including: the probability of encountering a covey (p), where p is a function of the effective area hunted (a) divided by that available (A). Thus, a, is a product of the velocity of hunter movement (v), hours spent hunting (h), and the effective width of the hunting zone (w). Velocity and hours spent hunting are easy to quantify, however, estimating w is more difficult and to-date not undertaken. We focused on w, specifically w_{ded}, the distance a dog detects a covey assuming the covey is stationary. We assume stationarity such that evasive behaviors can be estimated separately from the olfaction process. The objective of our experiments was to estimate the influence of weather on w_{ded}. We used pen-raised bobwhites placed about 150 meters apart to simulate hunts ($n = 13$) on two study sites. A handler guided a single birddog through the course, downwind from birds, and recorded the distance from the pointed dog to caged birds. Dogs pointed birds ($n = 236$) at an average distance of 6.2 m (SD = 4.2). Wind speed was positively associated with detection distance ($r = 0.19$, $P < 0.01$), while temperature was negatively associated ($r = -0.18$, $P < 0.05$). The hunter-covey interface is a dynamic process driven by a myriad of factors. Our results suggest simple weather parameters influence the effective area hunted, therefore, affecting the kill rate that managers want to control.

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Key words: *Colinus virginianus,* covey, hunt, hunter-covey interface, northern bobwhite, pointing dog

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EVALUATING THE IMPACTS OF HUNTING PATHS ON NORTHERN BOBWHITE SURVIVAL, ECONOMIC COSTS, AND HUNTER SATISFACTION

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ABSTRACT

The amount and spatial configuration of habitat is known to influence the abundance, movements, resource use, and persistence of many species. As such, land managers must be judicious in their application of management actions to minimize its impact on wildlife while concurrently providing recreational opportunities. Mowing or roller-chopping is a common management technique implemented on intensively managed northern bobwhite (*Colinus virginianus*) plantations to increase hunter accessibility, provide travel corridors for pointing dogs, manage vegetation succession, among other benefits. Managers typically create hunting paths in a grid pattern at 30 ft spacing resulting in approximately 35% of vegetation removed prior to hunting season. However, the optimal spacing for paths is unknown and some concern exists over the presence of paths in general as they may facilitate predation. Our objectives were to determine how different densities of paths (i.e., reduced cover and increased edge) impacted northern bobwhite survival, quantify the costs per hectare of paths, and determine hunter satisfaction. We developed two path treatments (30 ft and 90 ft spacing) and a control (no paths) on Tall Timbers Research Station in Leon County, Florida. We radio-tagged a subset of northern bobwhites ($n = 150$), equally distributed within each treatment, and monitored survival in each treatment using radio-telemetry during the non-breeding season (October through April) in 2013-2016. We used Burnham's joint model within program MARK to compare survival of radio-tagged bobwhites among treatment groups. We analyzed data collected from a hand-held global positioning system used to delineate paths during creation to compute implementation cost. Hunter satisfaction was assessed using a pre- and post-hunt survey. Optimization will be used to determine which treatment achieves the greatest utility under current management objectives. Results of this research will provide managers information to make informed decisions about the implementation of hunting paths under various management scenarios.

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Key words: hunting paths, program MARK, *Colinus virginianus*, northern bobwhite, survival estimation, hunter satisfaction

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EFFECT OF FIELD TRIALS ON NORTHERN BOBWHITE SURVIVAL AND HUNT QUALITY ON DIXIE PLANTATION

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ABSTRACT

The potential negative effects of horseback field trials on survival and post trial hunting quality of northern bobwhites (*Colinus virginianus*) have long been debated. Recent acquisition of Dixie Plantation (3,650 ha) by Tall Timbers Research Station provided a unique opportunity to evaluate this interaction as Dixie has been home to the Continental Field Trial since 1937. We monitored radio-tagged bobwhites annually ($n = 183$; ~20 coveys during fall/winter) on a core study area (640 ha) upon which a portion of the field trial was conducted during January 2015 & 2016. We estimated Kaplan-Meier survival of radio-tagged bobwhites on Dixie before, during, and after the field trial event as well as compared seasonal survival to bobwhite (N = 387) on nearby Tall Timbers Research Station (1,570 ha) during the same time period. Additionally, we recorded the number of coveys seen, coveys pointed, and shots fired during each half-day hunt ($n = 133$) to evaluate hunt quality before and after the field trial. Bobwhite survival on Dixie was similar ($P>0.05$) during the two weeks prior to (0.89, SE = 0.026), during (0.93, SE = 0.023), and after (0.92, SE = 0.026) the field trial for the two years combined, as were seasonal survival curves between the two study sites for both years monitored. No differences ($P>0.05$) were observed in the number of coveys seen per half day hunt before (X = 11.78, SE = 0.39) compared to after (X = 12.35, SE = 0.44), covey rises shot before (X= 6.89, SE = 0.28) and after (X = 7.75, SE = 0.37), or number of shots fired before (X = 23.5, SE = 1.19) versus after (X = 24.11 SE = 1.26) the field trial. We were unable to detect any evidence that the type of disturbance generated by this field trial had any effect on either bobwhite survival or post trial hunting quality on our study area.

Citation: Sisson, D. C., and T. M. Terhune II. 2017. Effect of field trials on northern bobwhite survival and hunt quality on Dixie Plantation. National Quail Symposium Proceedings 8:282–286.

Key words: bird dogs, *Colinus virginianus,* field trial, hunting, northern bobwhite*,* radio-telemetry, survival

INTRODUCTION

The potential effects of frequent disturbance by bird dogs on coveys of wild northern bobwhite (*Colinus virginianus*; hereafter, bobwhite(s)) has been a concern of sportsmen and biologists for decades and has been debated in the literature as well as among the field trial community. Stoddard (1931) proposed that hunting pressure caused coveys to shift use to heavier cover, and Rosene (1969) who reported consecutive weeks of bird dog training caused coveys to abandon an area in Alabama. Klimstra (1972) likewise reported coveys abandoning an area in Illinois when subjected to heavy hunting pressure, contributing to declining hunting success over the course of the season. Kellogg et al. (1982) also reported that the percentage of bobwhite coveys found declined significantly with successive hunts in north Florida. Janvrin (1991) reported increased covey movement in response to heavy hunting pressure but no abandonment of home ranges. Taken collectively, the concern of the potential impact of increased activity be it hunting pressure, training dogs, or field trials is valid. A major difference exists however between hunting pressure and these type field trials as no birds are shot during the trials. Any effect on mortality then would have to come from the potential for increased disturbance associated with the trial itself. Radio-telemetry studies of field trials, however, have revealed coveys to be generally unaffected (Dimmick and Yoho 1972) or the disturbance to be inconsequential (Wiseman 1977).

More recent concerns arose as bobwhite populations declined throughout their range and many field trials began to switch from wild bobwhites to pen-raised quail. To address these concerns, Kreh (1997) examined bobwhite movements, habitat use, and survival at the National Championship Field Trial on the Ames Plantation in Tennessee. Kreh (1997) found that in response to the field trial disturbance coveys would shift to heavier cover within their home range, but that survival was unaffected. He also concluded that the decline in wild bobwhite numbers on the property was not associated with field trial activities. While no detrimental impacts to bobwhite survival have been documented by any of these previous studies, none of them have addressed the potential impact of field trials on subsequent hunt success and/or quality.

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Unfortunately, there are few venues left in the southern U.S. where field trials are conducted exclusively on wild bobwhite. The Continental Field Trial is one of these rare exceptions and has been an integral part of the history of Dixie Plantation since 1937. Conducted annually during the last 2 weeks of January, the Continental Open All Age Championship is considered one of the top wild bobwhite field trials, routinely drawing nearly 150 of the top all-age bird dogs in the country. Consisting of morning and afternoon courses, each 20 km in length, the trial traverses most of the property on a daily basis. Wild bobwhite hunting is also an important part of Dixie Plantation's history as well as current land use. Revenue generated from lease hunting helps fund the operating budget on this working plantation. Lease hunters pay a premium for world class horseback wild bird hunting with the Florida season running from mid-November to early March. Care is taken to maintain the hunt quality by not hunting the same area more than once every two weeks and having a conservative harvest.

The recent gifting of Dixie Plantation to Tall Timbers Research Station & Land Conservancy, along with the ramped up wild bobwhite hunting program initiated, caused some concern from both the field trial community and the lease hunters. Since the two-week long trial occurs during hunting season each year in late January, lease hunters expressed concern about the impact the daily disturbance during the trial may have on bobwhite survival and post-trial hunt quality. Likewise, the field trial community was concerned about potential effects increased hunting pressure might have on the ability of the dogs to locate and point quail during the trial. As such, as part of a larger research effort on Dixie Plantation, we initiated research using radio-telemetry to evaluate the effect of the field trial on bobwhite survival and the subsequent hunt quality following the event.

STUDY AREA

Dixie Plantation has been a privately owned quail hunting property since 1926. The property was gifted to Tall Timbers Research Station & Land Conservancy in December of 2013, which now operates the property as Dixie Plantation Research, LLC. The objectives of the property are to: 1) maintain a high wild northern bobwhite population for hunting and field trials; 2) protect and enhance the ecological, cultural, and historical values; and, 3) conduct research and education in wildlife management.

Dixie Plantation is located in Jefferson County, Florida with the Aucilla river swamp as the western boundary and the Georgia state line the northern boundary. There are 720 ha of protected wetlands much of which is in the river swamp as well as ephemeral wetlands dotted throughout the uplands. There are approximately 400 ha of intensively managed planted pines and 220 ha in row crop agriculture/hay. Most of the remaining acreage (approx. 2,300 ha) is mature upland pine forest intensively managed for bobwhite quail hunting and field trials. Management practices include maintaining a low pine basal area, hardwood removal, frequent prescribed fire, roller chopping, mowing, herbicide spraying, and seasonal disking. Additional management practices include control of mammalian nest predators and year round supplemental feeding. These management practices result in a wild bobwhite population at Dixie that routinely exceeds 2.5 birds/ha as well as excellent habitat for many game and non-game wildlife species indigenous to the area.

A designated core research study area was developed on 640 ha in the heart of the property (Figure 1). This area is representative of the uplands on the property and is traversed by both the morning and afternoon field trial courses. Because the field trial covers the whole property, there was no opportunity to have a control study area directly on Dixie Plantation. Therefore, we used ongoing telemetry monitoring of bobwhites at Tall Timbers property, located 35 miles due west, as a control to compare survival curves through the fall-spring season. Tall Timbers (1568 ha), located in Leon County, Florida, is in the same physiographic region, part of the same landscape of private quail properties, and has a similar management regime maintained by frequent fire and low timber volume with mostly old-field groundcover (Carver et al. 2001). Bobwhite populations here also routinely exceed 2.5 birds/ha (Palmer et al. 2002).

METHODS

Monitoring

A year round sample of radio-tagged bobwhites has been maintained on Tall Timbers property since 1985 and on the Dixie study area since the spring of 2014. We trapped bobwhites 1 to 3 times a year (January, March, and/or October) in baited funnel traps (Stoddard 1931). All birds were weighed, sexed, aged, and leg banded with a subset outfitted with a 6-gram pendant style transmitter containing an activity switch (Holohil Systems. LTD., Ontario, Canada). Trapping, handling, and marking procedures were consistent with the guidelines in the American Ornithologists Union Report of Committee on the Use of Wild Birds in Research (American Ornithologists Union 1988) and the protocol was approved by the University of Georgia Institutional Animal Care and Use Committee, IACUC. On Dixie we deployed 5-6 transmitters in approximately 20 different coveys, evenly distributed across the core research area, each year in October. Similarly, more than 20 well distributed coveys were radio-tagged and monitored on Tall Timbers. All birds were monitored 2-4 times per week throughout the winter with additional emphasis and effort given to the weeks just prior to, during, and after the field trial. Previous analysis of radio-tagged birds on our study areas using the same procedures have revealed no effect of capture and handling or radio-handicapping; and that no censor period is needed

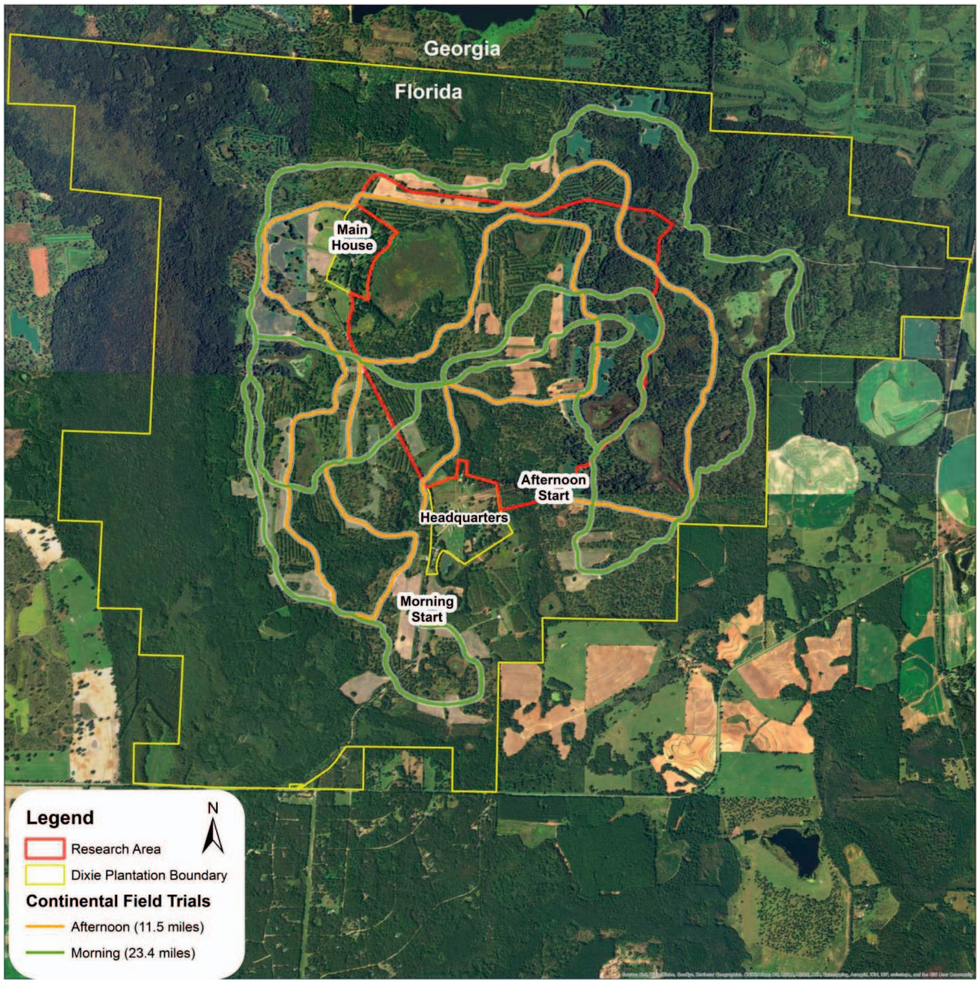

Fig. 1. Field Trial Courses and core research area (outlined in red) on Dixie Plantation in Jefferson County, Florida.

(Palmer and Wellendorf 2007, Terhune et al. 2007, Sisson et al. 2009).

Field Trial Disturbance

The disturbance created by the field trial was most similar to that described by Dimmick and Yoho (1972) and Kreh (1997) at the National Championship on Ames Plantation. The Continental was conducted each year beginning the third Monday in January and lasted until all dogs ran, usually about 14 consecutive days. Dog handlers used horseback to monitor braces of 2 dogs each with interchanging braces running for three hours in the morning and three hours in the afternoon. Separate morning and afternoon courses are 19-24 km in length with 7-8 km of each course overlapping the core research area (Figure 1). The courses are run the same time daily over the same route. They are traversed at a rapid pace as the Continental is an all-age stake, which means dogs are judged on their ground race and stamina as well as in finding game and holding steady to wing and shot. No birds are shot during the trial although a blank gun is fired each time there is a covey pointed and flushed. In addition to the dogs, there is a mounted dog handler and scout for each dog, two judges, a reporter, marshals, and spectator gallery each day. Total mounted participants can range from 20-50 depending on the day. We used records published in the American Field Magazine to evaluate the number of coveys pointed per 3 hour half day during the field trial.

Bobwhite Hunting

Hunts were conducted from horseback with 2 dogs on the ground at a time, a hunting wagon, and generally 6-8 horses carrying dog handlers, hunters, and guests. Each half-day hunt lasted approximately 3 hours and were systematically rotated across the 12 hunting courses on the property. A Dixie employee was present on each hunt as a guide and to collect data from the hunt. Data collected for each half day hunt included the total number of coveys seen by the party, number of coveys that were pointed by the dogs, number of shots fired, number of birds killed, and the sex, age, and weight of each harvested bird. Tall Timbers property is also hunted annually but was not hunted during the two weeks that the trial occurred at Dixie. Harvest was conservative and similar on both properties at a rate of less than 15% of the fall population.

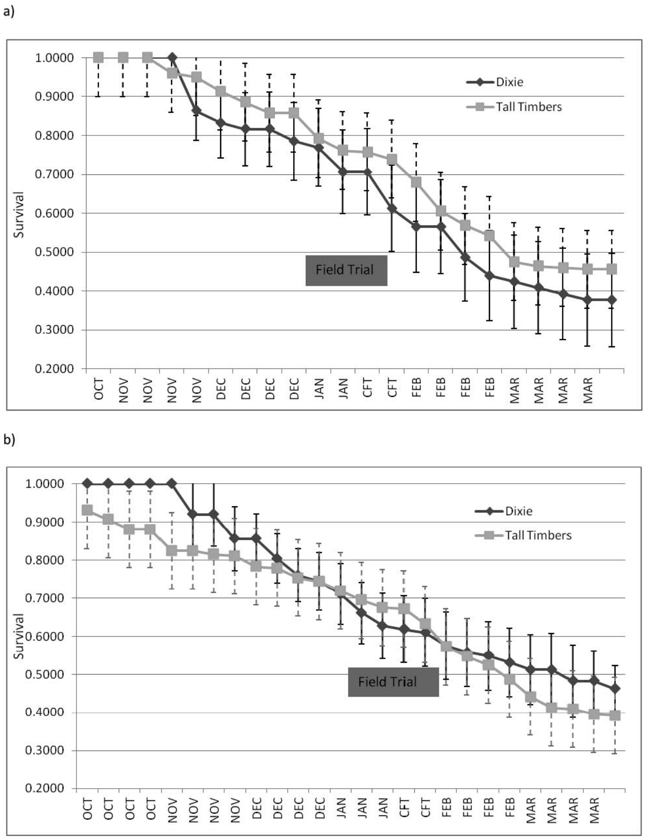

Fig. 2. Kaplan-Meier survival curves and 95% CI's show that survival of northern bobwhite did not differ between Dixie Plantation in Jefferson County, Florida and nearby Tall Timbers Research Station in Leon County, Florida during: a) October 2014-March 2015, and b) October 2015 – March 2016.

Statistical Analysis

We calculated seasonal survival estimates for the fall-winter period (1 Oct – 31 Mar) for both sites using the Kaplan-Meier staggered entry method (Kaplan and Meier 1958, Pollock et al. 1989) which allowed for inclusion of additional birds during the study and the censoring of others due to radio failure or emigration. Survival curves were compared between years and among treatments using log-rank tests (Pollock et al. 1989). We used the same methods to compare survival for two week intervals before, during, and after the trial. To evaluate data on hunt quality (coveys, points, and shots) between the hunts occurring before and after the field trial each year and for the two years combined, we calculated standard error of the means following Payton et al. (2003) and Schenker et al. (2001) and interpreted statistical and biological differences using 95% confidence intervals (Schenker et al. 2001, Williams et al. 2002, and Payton et al. 2003).

RESULTS

We monitored 570 radio-tagged bobwhites during the two over-winter seasons; 183 on Dixie and 387 on Tall Timbers. Bobwhites on Dixie had marginally lower survival than those at Tall Timbers during 2014-2015, but had marginally higher survival in 2015-2016 (Figure 2). However, log-rank tests showed no difference in survival distributions between sites for either year ($x^2 = 1.77$, df = 1, $P = 0.183$, and $x^2 = 0.493$, df = 1, $P = 0.472$, respectively). Over-winter survival in 2015 was 0.393 (SE = 0.06) on Dixie and 0.46 (SE = 0.03) at Tall Timbers, but was 0.48 (SE = 0.04) on Dixie and 0.40 (SE = 0.03) at Tall Timbers in 2016. Bobwhite survival was similar ($P>0.05$) on Dixie for the two-week period prior to, during, and after the field trial both years, and for the two years combined (Table 1). Data were collected on 133 half day hunts during the two hunting seasons, 78 prior to and 55 after the Continental Filed Trial. We did not detect a difference either year or for the two years combined between number of coveys seen, coveys pointed, and shots fired before and after the trial ($P>0.05$)(Table 1).

DISCUSSION

Our results confirm those from previous work demonstrating little to no effect on quail survival from the disturbance created by field trials (Dimmick and Yoho 1972, Wiseman 1977, Kreh 1997). Despite consistent activity and repetitive pressure from the field trial event, we believe the nature of this trial limits the overall impact on bobwhites. All-age bird dogs are judged as much on their range and stamina as hunting ability. Records of the trial show an average of 5-7 coveys pointed per half day with the gallery covering 19-24 km. On a typical hunt at Dixie, where dogs course more closely to hunters and cover ground more comprehensively, 7-8 coveys were pointed per half day with the hunt only covering approximately 8 km during a similar 3-hour time period. Our observations further support the finding of Dimmick and Yoho (1972) in that the daily variation in the actual areas that the dogs searched and the lack of repetitive and consistent disturbance of individual coveys contributed to this overall lack of effect. When these considerations are combined with the fact that no birds are being shot during the trial, it makes a compelling case that effect on survival is also minimal. While beyond the scope of this initial study, our preliminary observations seem to support the previous findings of coveys moving to heavier cover after repeated disturbance (Dimmick and Yoho 1972, Kreh 1997) but not leaving the area entirely as reported by Rosene (1969) and Klimstra (1972).

Previous studies have not evaluated the effect of these types of field trials on subsequent hunting success, but this was an important consideration of our work. We did not detect any negative effects on hunt quality in the parameters we measured (coveys seen, coveys pointed, shots fired) after the trial as compared to those conducted prior to it. However, this activity is quite different than heavy hunting pressure in which individual coveys are being moved and shot at repetitively which is known to make coveys harder to find (Kellogg et al. 1982) or move off the area entirely (Rosene 1969, Klimstra 1972). In our study, the hunts at Dixie were intentionally rotated throughout the courses to avoid frequent repetition of hunting the same ground and disturbing the same coveys

Table 1. Survival (± SE) and hunting success (coveys seen, coveys pointed, shots fired) (± SE) for northern bobwhites on Dixie Plantation in Jefferson County, FL before, during, and after the Continental Field Trial 2015 & 2016.

	Before	During	After
SURVIVAL			
2015	.90 ± .041	.87 ± .047	.92 ± .043
2016	.88 ± .034	.97 ± .019	.91 ± .033
Combined	.89 ± .026	.93 ± .023	.92 ± .026
HUNTING SUCCESS			
Coveys Seen			
2015	13.96 ± .60		13.28 ± .71
2016	10.75 ± .43		11.57 ± .51
Combined	11.78 ± .39		12.35 ± .44
Coveys Pointed			
2015	6.60 ± .41		6.84 ± .56
2016	7.04 ± .36		8.50 ± .46
Combined	6.89 ± .28		7.75 ± .37
Shots Fired			
2015	29.36 ± 1.8		22.96 ± 1.78
2016	20.7 ± 1.39		25.07 ± 1.79
Combined	23.5 ± 1.19		24.11 ± 1.26

which did not result in enough pressure to alter behavior of individual coveys.

The unique circumstances of the Continental Field Trial at Dixie provided us with the opportunity to test the general effects of these type of events on bobwhite survival and hunt quality but did not allow for replication. This lack of temporal and spatial replication limits the inferences that can be drawn, but do not undervalue the findings. The effect of field trials of differing duration and/or timing, or in lower density bobwhite populations may produce different effects. Additional study under varying circumstances as well as more detailed information on covey movements during these type events is warranted.

MANAGEMENT IMPLICATIONS

Field trial grounds with abundant wild bobwhite populations are rare on today's landscape. The lack of effect of this trial on post trial hunting quality and on bobwhite survival is significant and should comfort those in decision making roles in similar situations. These results show that if managed properly with all parties working together, hunting and field trials can co-exist on the same grounds when there is an abundant wild bobwhite population that is conservatively hunted and harvested.

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GENETIC DIVERSITY AND RELATEDNESS WITHIN AND AMONG NORTHERN BOBWHITE COVEYS IN SOUTH TEXAS

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ABSTRACT

Although biologists have studied northern bobwhite (*Colinus virginianus*) genetic diversity and population structure, there is little known about the genetic diversity, structure, and relatedness of their winter coveys. Both flexible mating strategies and the fall shuffle may have implications for inbreeding and genetic diversity in northern bobwhite populations. Our goal was to determine genetic diversity and relatedness for coveys on a private ranch in Jim Hogg County in South Texas. During the 2010–2011 and 2011–2012 hunting seasons, 96 northern bobwhites were sampled from 29 coveys. We analyzed 11 northern bobwhite microsatellite DNA loci, measured genetic structure with an Analysis of Molecular Variance and F_{ST}, and determined an inbreeding coefficient (F_i). We determined Queller and Goodnight's coefficients of relatedness (R) and then used a maximum-likelihood algorithm in COLONY to assign relationships (parent–offspring, full siblings, and half siblings). Most genetic variation (92%) was within coveys. The overall F_{ST} was 0.073, indicating moderate genetic structure among coveys. Relationship coefficients ranged from –0.82 to 1.00 but most of the bird pairs were unrelated ($R = –0.004 \pm 0.002$ SE). In 2010–2011, COLONY assigned 130–149 half sibling, 1–4 full sibling, and 0–3 parent–offspring pairs ($n = 2{,}887$, 5 trials, probability >0.99). Thirteen coveys (56%) had related individuals ($n = 20$ pairs). In 2011–2012, COLONY assigned 5–10 half sibling and 1 full sibling pairs ($n = 161$). Two coveys (33%) had related individuals (2 pairs). The occurrence of relatives in different coveys suggests that the fall shuffle is effective at mixing families and the high half sibling count among coveys may suggest polygamy. These strategies may help northern bobwhite populations maintain moderate genetic diversity.

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Key words: *Colinus virginianus,* covey dynamics, full sibling, half sibling, northern bobwhite, relatedness, South Texas

Flexible mating strategies and the fall shuffle are understood for northern bobwhite (*Colinus virginianus*). However, little is known of their effects to genetic diversity, covey structure, and relatedness of coveys. The northern bobwhite employs polyandry (Burger et al. 1995, Faircloth 2008) and male incubation of nests (Stoddard 1931, Lehmann 1984, Curtis et al. 1993). As nesting tapers off, family units will gradually form heterogeneous groups, or coveys. In late September, northern bobwhite individuals often move among coveys and the exchange of covey members is termed the "fall shuffle" (Lehmann 1984:36).

Repeated observations of color-banded birds and molecular analyses have shown that polygamy is a fairly common occurrence in many bird species. For males, having multiple mates is advantageous because of the opportunities to have more offspring and pass on genes (Freeland 2005:202; Pearson et al. 2006). Females may benefit from mating with multiple males to ensure fertilization and fitness where male quality varies (Griffith et al. 2002). Females also may benefit from the assistance of males in tending offspring, which raises the offsprings' survival chances and thus the female's reproductive fitness (Freeland 2005:202). In *r*-selected species, male

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incubation of the nest may allow the female to produce a second clutch, again improving her fitness (Freeland 2005:204).

Lack (1968:103) characterized the New World quail (Odontophoridae) as monogamous. However, subsequent studies have revealed the group to be polygamous, where male incubation and brood care are common (Sibley 2001). For instance, Burger et al. (1995) found that 71% of northern bobwhite females engaged in polyandrous mating at some point during the breeding season. Polyandry may be facilitated by male incubation of nests: if the male incubates the nest, the female is then able to have a second nest with a different male. Male incubation of nests was documented for the northern bobwhite in early natural history studies (Stoddard 1931:30, Lehmann 1984:87) and occurs in 20–30% of nests (Brennan et al. 2014). Curtis et al. (1993) noted that a female may renest with a different male if the first male incubates the eggs or tends the brood, sometimes within days after laying her initial clutch. These strategies may result in a large number of siblings in a given year.

The fall shuffle affects the distribution of the related northern bobwhites within and among coveys. According to Lehmann (1984:19), the fall shuffles in South Texas finish by November, at which point most northern bobwhites have sorted themselves into winter coveys composed of 6–16 individuals. Northern bobwhites have a greater survival rate when the covey size is 11–12 birds (Williams et al. 2003). This optimal covey size is maintained over the winter as large coveys lose members and small coveys gain members (Lehmann 1984:appendix E). Living in coveys is advantageous for locating food and evading predators (Williams et al. 2003). During cold periods, northern bobwhites huddle together in the covey to conserve heat (Case 1973, Lehmann 1984:11, Roseberry and Klimstra 1984). Finally, winter coveys often have fairly even sex ratios and provide access to potential mates in the spring (Lehmann 1984:50).

Promiscuity and shuffling of individuals among coveys may allow northern bobwhite populations to retain genetic variation despite loss of habitat and an overall decline in census size throughout their range (Berkman 2012, Evans et al. 2013, Williford et al. 2014). Promiscuous mating can result in a greater effective population size than monogamous mating systems (Sugg and Chesser 1994), whereas the fall shuffle should increase gene dynamics within a population and reduce the chances of a local inbreeding (Leopold 1931). Inbreeding avoidance is crucially important to a species that exhibits short-distance movements, such as the northern bobwhite (Stoddard 1931:182, Leopold 1933:75). For example, Agee (1957) found that during fall males tended to join the coveys closest to their home range. A combination of promiscuous mating and social group structure might contribute to the retention of genetic diversity and perhaps to gene flow. To date, there is little quantitative information on the genetic composition of northern bobwhite social groups.

Our overall objective was to determine genetic diversity, genetic structure, and relatedness within and among northern bobwhite coveys on a private ranch in Jim Hogg County in southern Texas. We developed 3 research hypotheses focused on the potential patterns of genetic relatedness within and among coveys. First, we hypothesized that families remaining intact through the shuffle and into the winter should result in coveys with full siblings and parents, but if families were separated during the fall shuffle, full siblings and half siblings would be distributed among coveys rather than within coveys. Secondly, we expected a gradient of relatedness over time. At the beginning of the winter, coveys should consist of related individuals, but due to the transfers among coveys and the effects of hunting and predation, related individuals should be dispersed among coveys by the end of winter. Finally, we hypothesized that the degree of promiscuity should be reflected in the ratio of full siblings to half siblings in the sample. For example, if northern bobwhite females are monogamous during their first nesting attempt and there are 10 females with nests and the clutch size = 10 eggs in each nest, 9% (450) of the pairs should be full siblings (Fig. 1). If 30% of the females then lay second nests with different males, we would expect 7% (585) full sibling pairs and 3.6% (300) half sibling pairs. This is an estimated 2 : 1 ratio of full to half siblings (Fig. 1).

STUDY AREA

We conducted the study on a 3,558-ha private ranch near Hebbronville, Jim Hogg County, Texas (Fig. 2). Temperatures vary from 20° C (68° F) in winter to 36° C (97° F) in summer. Average annual rainfall is 60 cm (24 in; 1980–2010, http://www.ncdc.noaa.gov/). Most of the land can be classified as sandy mesquite (*Prosopis glandulosa*) savanna, sandy mesquite woodland, and deep sand grassland (Elliott 2011). These plant communities are characterized by native (gulfdune paspalum [*Paspalum monostachyum*], red lovegrass [*Eragrostis secundiflora*], tanglehead [*Heteropogon contortus*], and seacoast bluestem [*Schizachyrium scoparium var. littorale*]) and nonnative grass species (Coastal bermudagrass [*Cynodon dactylon*], Lehmann lovegrass [*Eragrostis lehmanniana*], and buffelgrass [*Pennisetum ciliare*]). Forbs include camphor weed (*Heterotheca subaxillaris*), camphor daisy (*Rayjacksonia phyllocephala*), and partridge pea (*Chamaecrista fasciculata*). Elliott (2011) also defined these areas as having patchy overstories of woody species (honey mesquite, huisache [*Acacia farnesiana*], and blackbrush [*Acacia rigidula*]). Prickly pear (*Opuntia engelmannii* var. *lindheimeri*) can be found throughout the area. Shallow scrubland, row crops, disturbed grasslands, and mesquite woodland are also present (Elliott 2011, Texas Ecological Land Classification Project).

Management of the ranch was targeted at habitat for northern bobwhite and white-tailed deer (*Odocoileus virginianus*) hunting operations. Habitat management efforts included roller chopping, herbicide treatments for invasive grass, disking, and rotational grazing of cattle ranch manager, personal communication).

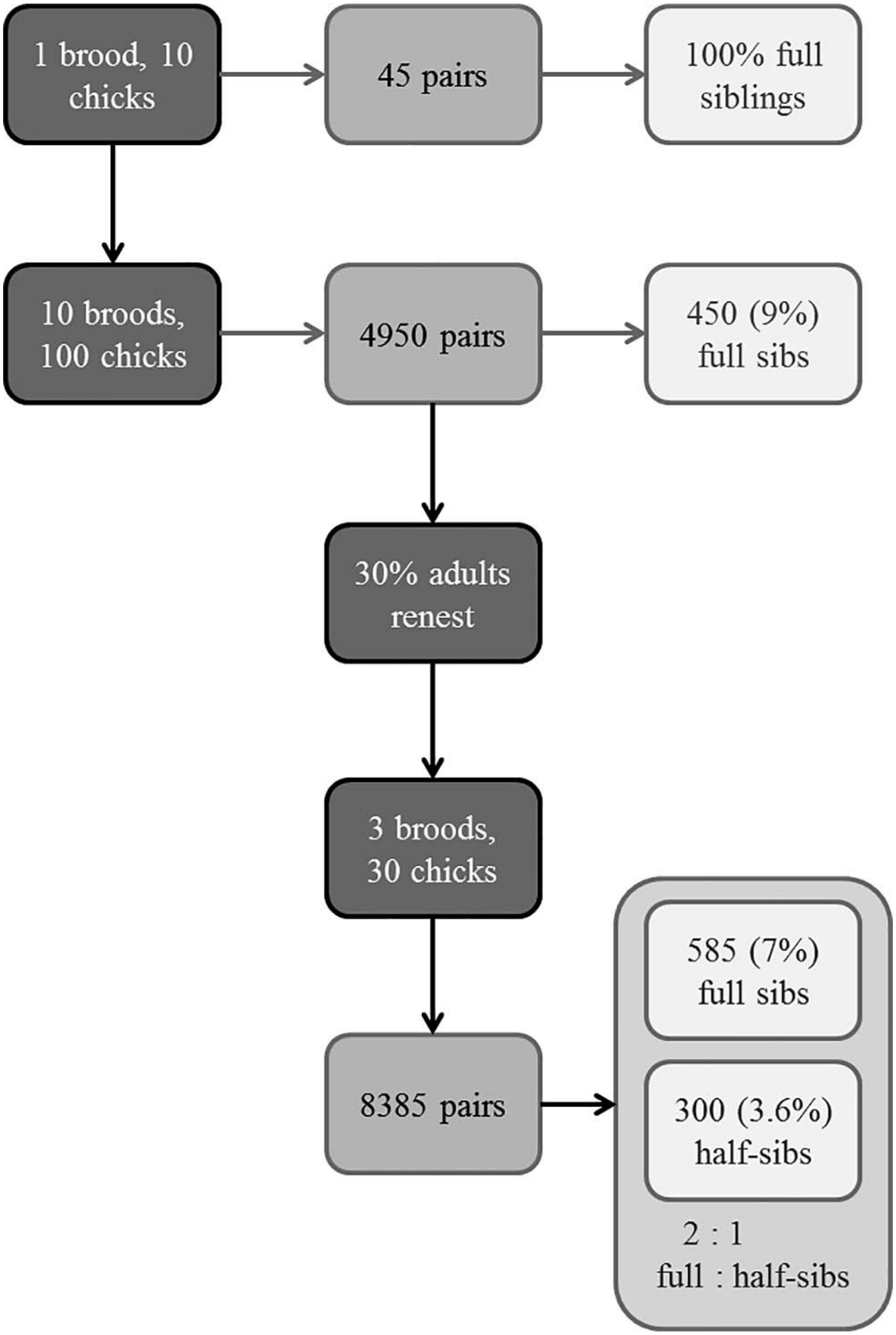

Fig. 1. A hypothetical model where northern bobwhites (*Colinus virginianus*) are monogamous during their first mating, and each clutch produces 10 offspring, and there are 10 initial nests. If 3 females (30%) then lay second broods fertilized by a different male, these would be half siblings to the full siblings of the first brood.

METHODS

Data Collection and DNA Amplification

We sampled coveys via hunter-harvest during 2 hunting seasons (Dec–Feb of 2010–2011 and 2011–2012) on the ranch. Hunters recorded the time and date of harvest, sex of the birds, and whether birds were taken from the same covey. We extracted DNA from all individuals representing coveys where ≥ 3 birds were harvested. This consisted of 3–5 samples/covey. We classified individuals as juvenile or adult based on presence or absence of buffy tips on the primary coverts

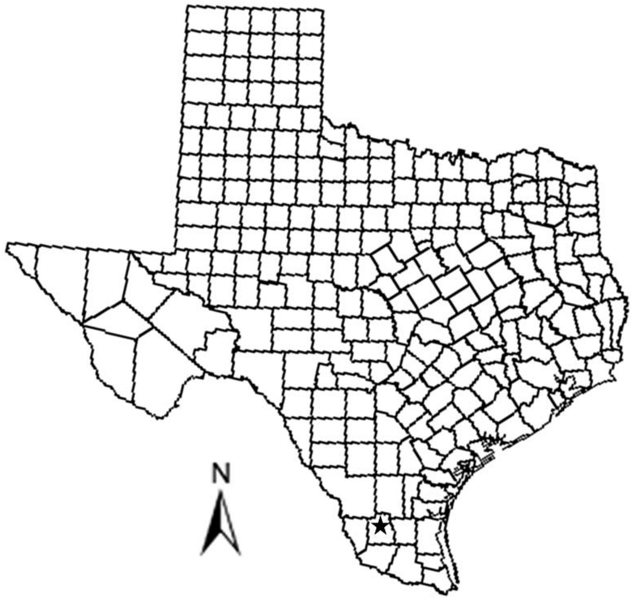

Fig. 2. The ranch, denoted with a star, located in Jim Hogg County, South Texas. Northern bobwhite (*Colinus virginianus*) samples were collected in the winters of 2010–2011 and 2011–2012 to examine covey genetic relatedness.

(Rosene 1969:54). We removed a portion of tissue from each wing and extracted DNA with a commercial kit (DNeasy, Qiagen, Inc., Valencia, CA, USA).

We amplified 13 microsatellite DNA loci (Schable et al. 2004, Faircloth et al. 2009). We amplified the DNA using polymerase chain reaction (PCR) in 10-μL volumes containing 1.5 μL DNA extract, 5.0 μL AmpliTaq Gold PCR Master Mix (Applied Biosystems, Carlsbad, CA), 0.5 μM of primer (forward and reverse), and 2.5 mM $MgCl_2$. For Schable et al.'s (2004) microsatellites, all PCR protocols started with an initial denaturation step of 94° C for 10 min. We amplified loci Quail 10, Quail 21, Quail 22, Quail 24, and Quail 26 with 21 cycles of 94° C for 20 sec, an annealing temperature of 59° C for 30 sec, and elongation at 72° C for 1 min (Schable et al. 2004). The protocol for Quail 23 differed only in the annealing temperature: 54.4° C. For Quail 14 and Quail 32, we used a touchdown protocol with 2 steps. The first step consisted of 21 cycles of 94° C for 20 sec, a starting annealing temperature of 60° C that decreased 0.5° C with each cycle for 30 sec, and elongation at 72° C for 1 min. The second step consisted of 10 cycles of 94° C for 30 sec, 50° C for 30 sec, and elongation at 72° C for 1 min. The PCR protocols for all of Schable et al.'s (2004) loci included a final extension at 72° C for 7 min.

For microsatellite loci in Faircloth et al. (2009), all PCR protocols included an initial denaturation step at 95° C for 10 min. For CV–PBA4 and CV–PCF5, we used a 2-step touchdown protocol. The first step consisted of 20 cycles of 95° C for 20 sec, a starting annealing temperature of 65° C that decreased 0.5° C each cycle for 30 sec, and elongation at 72° C for 90 sec. The second step consisted of 20 cycles of 95° C for 20 sec, 60° C for 30 sec, and elongation at 72° C for 90 sec (Faircloth et al. 2009). For CV–PBA7, CV–PC1F2, and CV–PC1F3, we used a similar touchdown protocol with an initial annealing temperature of 60° C in the first step and 50° C in the second step. We included a final extension at 72° C for 10 min for all loci (Faircloth et al. 2009). We amplified all microsatellites on ABI 2720 (Applied Biosystems, Foster City, CA, USA) and MyCycler (Bio-Rad, Hercules, CA, USA) thermal cyclers. We combined PCR products with denaturing formamide and ROX ^{TM} size standard for separation and detection of fragments, and loaded the samples on an ABI Prism 3130 Genetic Analyzer. We genotyped samples with Gene Mapper 4.0 (Hitachi, Applied Biosystems). We determined the genotyping error rate by reamplifying and regenotyping 30 randomly selected samples.

Data Analysis

We estimated the rate of null alleles with ML-NullFreq (Kalinowski and Taper 2006). We quantified genetic diversity with allelic richness (HP-Rare v. 1.1; Kalinowski 2005) and heterozygosity (ARLEQUIN 3.5; Excoffier and Lischer 2010). We tested for significance of departure from Hardy–Weinberg expectations with 10,000 random permutations of alleles among individuals. We partitioned genetic structure within and among coveys with an Analysis of Molecular Variance (Weir and Cockerham 1984) and F_{ST}. We tested for significant departure of global F_{IS} and F_{ST} from 0 by jackknifing over loci. These analyses were performed in ARLEQUIN 3.5 (Excoffier and Lischer 2010). We determined an individual inbreeding coefficient (F_i, the probability of identity-in-state between genes within individuals; Ritland 1996, Hardy 2003) for each covey with SPAGeDi v. 1.4 (Hardy and Vekemans 2002). Here, F_i is determined by the probability of identity-in-state between genes within individuals and the probability of identity-in-state between random genes from a reference population (Hardy 2003).

We used multiple approaches to determine genetic relatedness among individuals and among coveys. This is because the sampling variance of the relatedness estimator often results in a departure of the estimate from expected values of identity by descent (DeWoody 2005). First, we determined pairwise coefficients of relatedness (R, Queller and Goodnight 1989) with SPAGeDi v. 1.4 (Hardy and Vekemans 2002) and determined parent–offspring or full siblings (expected $R = 0.50$) and half siblings (expected $R = 0.25$). We used a 99% confidence interval to establish the lower and upper bounds of what we considered a parent–offspring, full sibling, or half sibling relationship. We then determined full sibling, half sibling, and parent–offspring pairs using a full pedigree maximum-likelihood algorithm in COLONY v. 2.0.4.5 (Wang 2004). We treated the mating system as polygamous for both sexes, with no inbreeding, and no prior knowledge of sibship size. We ran the maximum likelihood algorithm 5 times, varying length of run (short vs. medium) and used different random number seeds.

Finally, we generated R-values for all pairs with COANCESTRY v. 1.0 (Wang 2011). COANCESTRY

Table 1. Number of alleles (A), allelic richness (A_R; $k = 2$ genes), observed (H_O) and expected heterozygosity (H_E), and individual inbreeding coefficient (F_i) for northern bobwhite (*Colinus virginianus*) on a private ranch in South Texas (2010–2012). Ninety-six birds in 29 coveys were sampled.

	A	A_R	H_O	H_E	F_{is}	F_i	P (F_i)	Reference
Quail 10	12	1.77	0.50	0.72	0.37	0.40	**0**	Schable et al. 2004
Quail 21	11	1.74	0.46	0.65	0.32	0.48	**0**	Schable et al. 2004
Quail 22	17	1.90	0.87	0.87	–0.04	0.04	0.195	Schable et al. 2004
Quail 23	17	1.86	0.93	0.84	–0.13	–0.07	0.079	Schable et al. 2004
Quail 24	8	1.60	0.59	0.58	–0.10	0.04	0.584	Schable et al. 2004
Quail 32	9	1.54	0.62	0.57	–0.10	0.00	0.937	Schable et al. 2004
CV–P1A7	8	1.71	0.75	0.72	–0.06	–0.04	0.472	Faircloth et al. 2009
CV–PBA4	10	1.70	0.61	0.69	0.09	0.20	**0.002**	Faircloth et al. 2009
CV–PCF5	17	1.81	0.63	0.74	0.17	0.22	**0**	Faircloth et al. 2009
CV–PIF2	11	1.86	0.64	0.80	0.30	0.37	**0**	Faircloth et al. 2009
CV–PIF3	12	1.79	0.72	0.73	–0.03	0.07	0.158	Faircloth et al. 2009

estimates R with 5 moment estimators (Queller and Goodnight 1989, Li et al. 1993, Ritland 1996, Lynch and Ritland 1999, Wang 2002) and 2 likelihood algorithms (Milligan 2003, Wang 2007). We allowed the TrioML likelihood method to account for inbreeding. We compared these different estimators with Pearson's correlations. Results are presented as ±SE unless otherwise noted.

RESULTS

Over the course of the study period, we sampled 96 birds representing 29 coveys. The winter (Dec–Feb) of 2010–2011 followed a moist year (Palmer Modified Drought Index, http://www.ncdc.noaa.gov) and northern bobwhite population numbers were high. During this season, we collected 77 birds representing 23 coveys. The following summer, South Texas experienced a severe drought and the ranch reduced its harvest. As a result, we only collected 19 birds from 6 coveys. We pooled the samples from 2011 to 2012 with the 2010–2011 data for analysis. We calculated an error rate of 0.049, averaged over loci, and used the genotyping error rate in COLONY runs. In 2010–2011, most birds were juveniles (40 M, 30 F) rather than adults (4 males, 3 female). In 2011–2012, all birds were adults (9 M, 10 F). Average number of samples per covey was 3.27 ± 0.12 birds.

Table 2. Analysis of Molecular Variance for northern bobwhite (*Colinus virginianus*) coveys on a private ranch in South Texas, 2010–2012.

Source of variation	df	Sum of squares	Variance components	% of variation
2010–2011				
Among coveys	22	128.17	0.31 Va	7.49
Within coveys	131	477.84	3.84 Vb	92.51
Total	153	606.01	4.15	
		$F_{ST} = 0.075$	$P < 0.001$	
2011–2012				
Among coveys	5	24.73	0.22 Va	5.37
Within coveys	32	108.79	3.90 Vb	94.63
Total	37		4.12	
		$F_{ST} = 0.054$	$P < 0.001$	
Over all years				
Among coveys	28	160.43	0.30 Va	7.30
Within coveys	163	586.63	3.85 Vb	92.70
Total	191	747.07	4.16	
		$F_{ST} = 0.073$	$P < 0.001$	

Two microsatellite loci were not included in the analyses. Quail 14 was removed from the set because of a very low heterozygosity and low polymorphism and Quail 26 was removed because of the amount of missing data from nonamplification. Out of the 11 remaining loci, MLNull-Freq identified 2 markers as having potential null alleles, Quail 10 and Quail 21. These were included in subsequent analyses to provide additional genetic information for parentage analyses.

Allelic richness ranged from 1.54 to 1.90 and heterozygosity ranged from 0.46 to 0.93, over 96 samples (Table 1). F_{IS}, averaged over all loci, was 0.117. The inbreeding coefficient (F_i) ranged from –0.017 to 0.48; therefore, there was a deficiency of heterozygotes for Quail 10, Quail 21, CV–PBA4, CV–PCF5, and CV–PIF2 (Table 1). The overall F_{ST} was = 0.073, $P < 0.001$, indicating moderate structure among coveys. Most variation was within the coveys (Table 2).

Pairwise relationship coefficients (R) ranged from –0.82 to 1.00, average $R = –0.004 \pm 0.002$. Relatedness within coveys was greater in 2010–2011 (0.10 ± 0.002, $n = 121$ pairs) than 2011–2012 (0.02 ± SE = 0.05, $n = 26$ pairs; Fig. 3). Among coveys, average relatedness was low in both 2010–2011 (–0.003 ± 0.003, $n = 4{,}815$ pairs) and 2011–2012 (–0.006 ± 0.012, $n = 272$ pairs). Relatedness of juvenile males and females within coveys was lower than relatedness of juvenile or adult birds among coveys (Fig. 4). Average relatedness of females within coveys (0.01 ± 0.06, $n = 17$ pairs) was lower than average relatedness of males within coveys (0.13 ± 0.04, $n = 34$ pairs). Average relatedness of females or males among coveys suggested most birds were not related (F –0.02 ± 0.007, $n = 745$ pairs, M –0.007 ± 0.006, $n = 1{,}396$ pairs; Fig. 4).

The 5 COLONY run results were similar in the number of assignments made for half siblings, full siblings, and parent–offspring (Table 3). COLONY

Table 3. Comparison of 5 COLONY runs and Queller and Goodnight's R to determine northern bobwhite (*Colinus virginianus*) relatedness in coveys of 2010–2011, 2011–2012, and across years. Probability of relatedness in COLONY $P > 0.99$. For Queller and Goodnight's R, parent–offspring / full siblings = 0.50, 99% CI = 0.492–0.508, and half siblings = 0.25, 99% CI = 0.247–0.253).

	Random number and length of run					
Relationship	1,234 Short	1,234 Medium	1,367 Short	1,810 Short	1,810 Medium	Queller and Goodnight's R
Within 2010–2011						
No. of pairs	2,887	2,887	2,887	2,887	2,887	2,887
Full siblings	2	4	1	1	4	12
Half siblings	149	139	137	136	130	111
Parent–offspring	0	3	0	1	0	0
No relationship	2,736	2,741	2,749	2,749	2,753	2,764
Frequency (%)						
Full siblings	0.07	0.14	0.03	0.03	0.14	0.42
Half siblings	5.16	4.81	4.75	4.71	4.50	3.84
Parent–offspring	0.00	0.10	0.00	0.03	0.00	0.00
No relationship	94.77	94.94	95.22	95.22	95.36	95.74
Full sibling : Half sibling	1 : 74	1 : 34	1 : 137	1 : 136	1 : 32	1 : 9
Within 2011 Season						
No. of pairs	161	161	161	161	161	161
Full siblings	1	0	0	0	1	3
Half siblings	5	8	9	10	7	10
Parent–offspring	0	0	0	0	0	0
No relationship	155	153	152	151	153	148
Frequency (%)						
Full siblings	0.62	0	0	0	0.621	1.86
Half siblings	3.10	4.97	5.59	6.21	4.35	6.21
Parent–offspring	0	0	0	0	0	0
No relationship	96.27	95.03	94.41	93.80	95.03	91.93
Full sibling : Half sibling	1 : 5				1 : 7	1 : 3
Among seasons						
No. of pairs	1,463	1,463	1,463	1,463	1,463	14,63
Full siblings or Parent–offspring	2	1	0	0	1	5
Half siblings	43	57	54	41	26	47
No relationship	1,418	1,405	1,409	1,422	1,436	1,411
Frequency (%)						
Full siblings or Parent–offspring	0.14	0.07	0	0	0.07	0.34
Half siblings	2.94	3.90	3.69	2.80	1.78	3.21
No relationship	96.92	96.03	96.31	97.20	98.15	96.45

assignments with probability >0.99 indicated relatives within 13 coveys (56.5%) in 2010–2011 (Fig. 5). From 2,887 pairwise comparisons of individuals, 130–149 pairs were half siblings, 1–4 pairs were full siblings, and 0–3 were parent–offspring pairs. Queller and Goodnight's R revealed a high ratio of half siblings ($R = 0.25$, 99% CI = 0.247–0.253) to full siblings ($R = 0.50$, 99% CI = 0.492–0.508), though the disparity was not as extreme (111 half siblings to 12 full siblings; Table 3). Most pairs (94–95%) were not related. Relatedness within coveys did not decrease over time ($n = 4$ coveys in Dec, 4 in Jan, and 5 in Feb). In 2011–2012, 161 pairwise comparisons resulted in 5–10 half siblings and 0–1 full sibling pairs (Fig. 6). The remaining pairs (94–96%) were not related. The high half sibling to full sibling ratio was supported again by Queller and Goodnight's R (10 half siblings, 3 full siblings; Table 3). Out of 1,463 pairwise comparisons among the years, 26–57 were half siblings, and 1–2 were either full siblings (1 from 2010–2011 and 1 from 2011–2012) or parent–offspring pairs where the juvenile was from 2010–2011 and the adult survived until 2011–2012 (Fig. 7). The remaining pairs (96–98%) were not related (Fig. 7).

We found that the methods used to generate relatedness estimates in COANCESTRY provided full: half sib ratios from 1 : 2 (TrioML) to 1 : 55 (DyadML) in 2010. In the 2011–2012 season, full:half sib ratio ranged from 1 : 1 (Rit) to 1 : 2 (DyadML). COLONY estimates were weakly correlated to the other relatedness estimators; however, all other relatedness estimators showed moderate to strong positive correlations (Table 4).

DISCUSSION

We detected low genetic diversity and fine–scale (2–12 km) genetic structure among coveys on our study site, potentially due to the presence of male relatives within coveys. However, genetic diversity and structure are strongly influenced by the sample size and sampling method. Hunters harvested 3–5 birds from a covey and

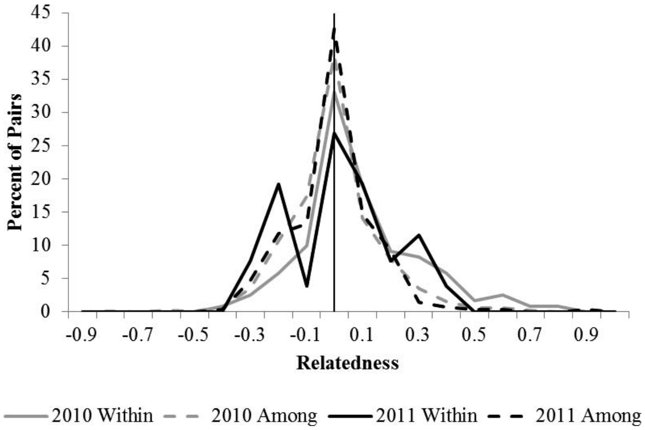

Fig. 3. Frequency of relationship coefficients (Queller and Goodnight's *R*) within and among northern bobwhite (*Colinus virginianus*) winter coveys, South Texas, 2010–2011 and 2011–2012. Average relatedness within and among coveys the first winter and among coveys the second year was low. Relatedness within coveys the second year should be interpreted with caution; this was the smallest group of pairwise comparisons (26 pairs).

then moved on to the next covey; live-trapping and sampling a full covey of ~12 birds would have yielded a more accurate estimate of genetic diversity than nonrandom sampling. Moderate fine-scale structure may indicate that the genetic diversity, already low, has some spatial pattern within the context of our study. Further, the F_i is determined in part by the probability of identity-in-state between random genes from a reference population (Hardy 2003) and our sampling method did not provide a true reference population.

We expected that northern bobwhite coveys would consist of related individuals, at least at the start of winter. However, related individuals were distributed among coveys throughout the winter. Further, we expected to find a gradient of relatedness over time for coveys, if northern bobwhites stayed in family groups through the fall shuffle and then proceeded to lose members over the course of the winter. Instead, relatedness within and among coveys did not change over the season. The moderate genetic structure of this population and the pattern of siblings (both half and full) spread throughout the coveys throughout the winter suggest that the fall shuffle may be distributing family members among coveys and that coveys continue to gain and lose members through the winter. We also expected that if northern bobwhite females were monogamous with respect to each clutch, one would expect an approximate ratio of 2 : 1 full to half siblings, even after accounting for second broods. In contrast, the ratio in 2010–2011 was 1 : 9–137 and in 2011–2012 it was 1 : 3–5. This high ratio of half siblings to full siblings suggests that promiscuity was common in this population.

Fall Shuffle and Mixing of Coveys

From the pattern of related individuals throughout coveys, it appears that the fall shuffle is an effective means of distributing northern bobwhites among coveys. This mixing among northern bobwhite families can start as early as late summer, if a male and his young from the first nest join the female with young from her second nest. Although the formation of and mixing of coveys is likely driven by the optimal number of individuals for survival (Lehmann 1984, Williams et al. 2003), if unrelated young are amalgamated into the group to further brood survival, as in Faircloth et al. (2005), this also effectively creates a mixed group. For example, Faircloth et al. (2005) noted most broods of 3–7-day-old chicks contained related young, but that for broods of 10–12-day-old chicks, brood amalgamation increased to 20–22%.

Covey size in northern bobwhite coveys usually ranges from 6–25 birds (Rosene 1969:91) but the optimal covey size is 11–12 birds (Lehmann 1984:23, Williams et al. 2003). Smaller coveys had lower individual survival and more movement as the covey sought to join with another covey. Larger coveys had lower individual survival and a decrease in individual mass (Williams et al. 2003). Lehmann (1984:23) found that in South Texas only 10% of coveys had <6 or >16 birds. Therefore, if the covey tries to hold its size at approximately 12 members, it likely will lose and gain individuals in the process (Lehmann 1984:43, Williams et al. 2003). Yoho and Dimmick (1972) documented this exchange to be around 1 bird every 3 days. Both Ellis et al. (1969) and Robel and Klopfenstein (1985) documented that northern bobwhite coveys would lose and gain personnel through the winter.

The fall shuffle is usually over by the end of November (Lehmann 1984) and, although hunting season is open, most hunters and ranch managers rarely hunt before December in South Texas. Hunting parties may cause individuals of a covey to scatter and the birds that survive the hunt may reform their covey or move to other coveys. This adds to the already dynamic status of winter coveys (Lehmann 1984). Therefore, although related birds may be within a covey at the beginning of the winter, they may not be in the same covey by the end of the winter.

Northern Bobwhite Promiscuity

The high ratio of half to full siblings in our study suggests that northern bobwhites are promiscuous, and perhaps more so than previously documented. One possible reason for promiscuity may be linked to double-brooding, which may evolve through 2 methods (Blomqvist and Johansson 1994). In monogamous species where the male begins to incubate, the female is "liberated" to develop a second nest. In species where one or both sexes are polygamous, a hen may have 2 nests from 2 separate males (Blomqvist and Johansson 1994). The high ratio of half siblings to full siblings observed in this study far exceeds the expected ratio produced under scenarios of multiple broods, unless the number of broods per female was far greater than ever documented. For such a high half sibling to full sibling ratio, northern bobwhites must display a high degree of promiscuity, which has been suggested from behavioral studies (Burger et al. 2005, Brennan et al. 2014) and documented by

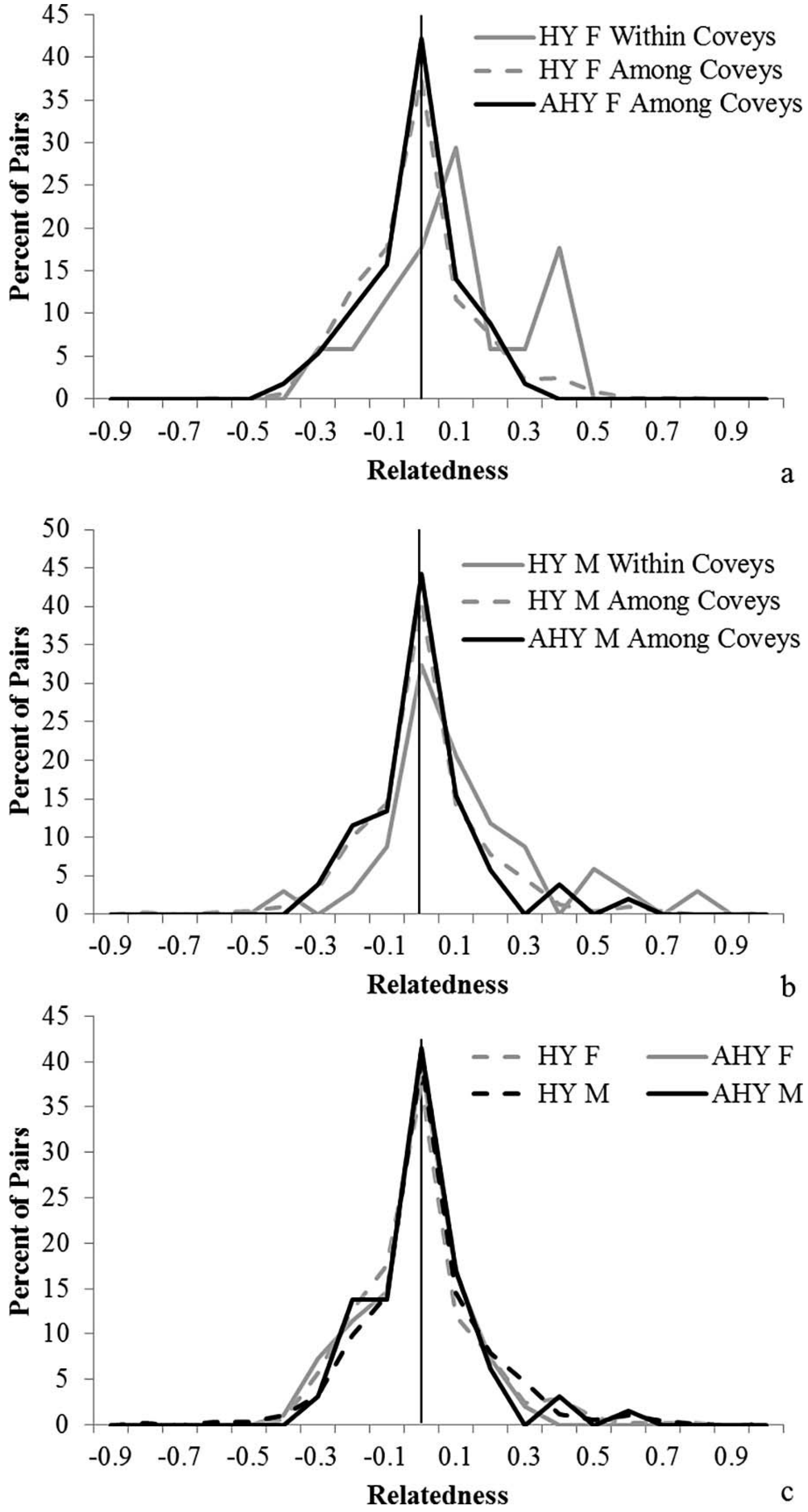

Fig. 4. Frequency of relationship coefficients (Queller and Goodnight's R) within and among northern bobwhite (*Colinus virginianus*) winter coveys. Frequency is shown for (a) juvenile (HY) and adult (AHY) females (F), (b) HY and AHY males (M), and (c) across age and gender groups.

Table 4. Comparisons of relatedness in northern bobwhite (*Colinus virginianus*) coveys: Queller and Goodnight relatedness computed with SPAGeDi, relatedness from COLONY, and 5 point estimators (Queller and Goodnight 1989, Li et al. 1993, Ritland 1996, Lynch and Ritland 1999, Wang 2002) and 2 likelihood ratios (Milligan 2003, Wang 2007) from COANCESTRY. Values represent Pearson's r, tests were significant at $\alpha = 0.05$, df = 4559.

	QG	COLONY	TrioML	Wang	LynchLI	LynchRD	Rit	QG	DyadML
QG	—	0.284	0.723	0.833	0.904	0.725	0.717	0.999	0.739
COLONY		—	0.384	0.274	0.263	0.378	0.362	0.287	0.383
TrioML			—	0.672	0.658	0.744	0.707	0.722	0.979
Wang				—	0.926	0.686	0.641	0.836	0.697
LynchLI					—	0.658	0.662	0.908	0.682
LynchRD						—	0.905	0.723	0.768
Rit							—	0.716	0.731
QG								—	0.738
DyadML									—

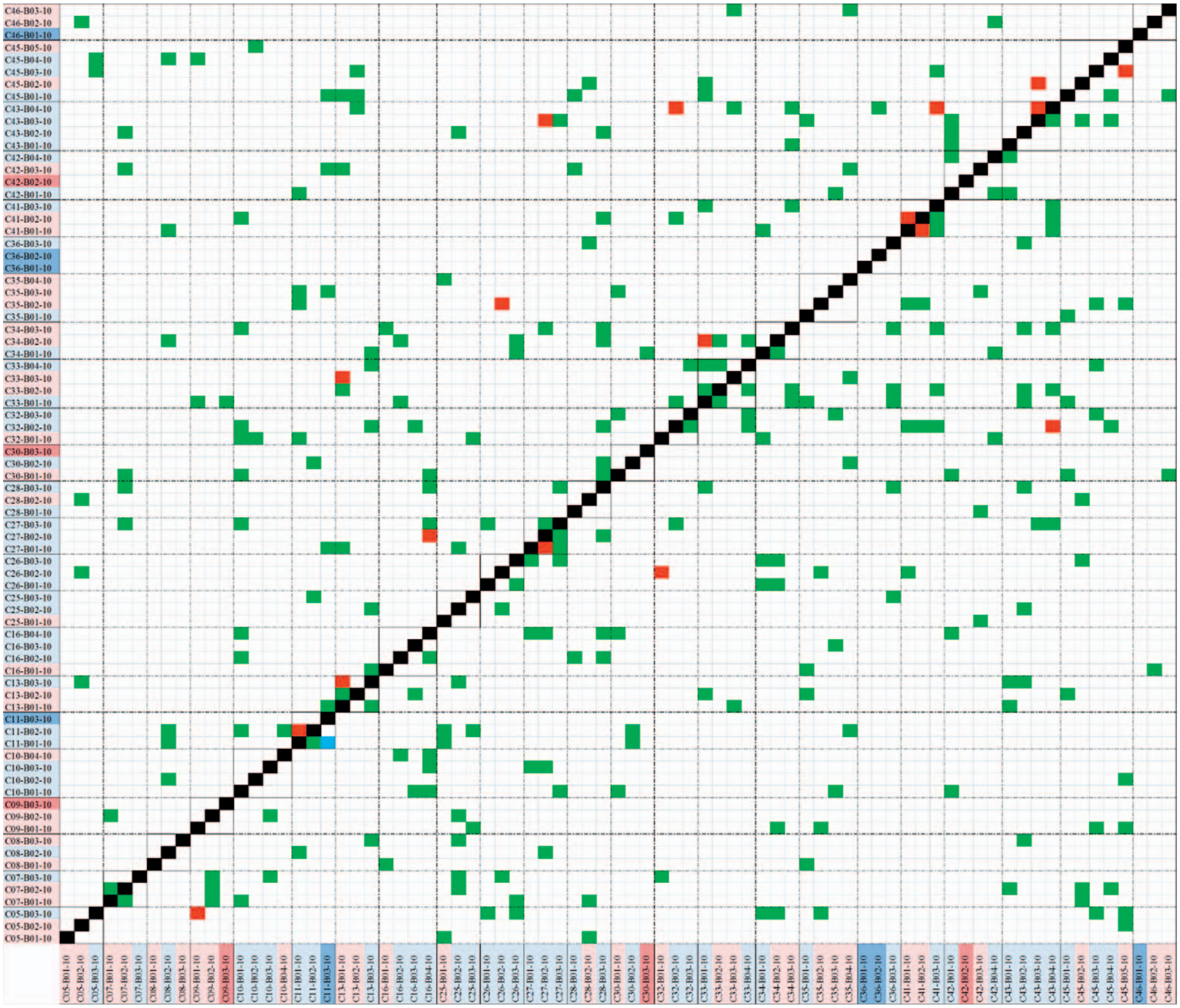

Fig. 5. Covey genetic relatedness for northern bobwhite (*Colinus virginianus*) in 2010–2011, South Texas. Probability of relatedness $\geq$0.99 from COLONY v. 2.0.4.5 (Wang 2004) is shown in the lower right of the matrix. Queller and Goodnight's R relatedness is shown above in the upper left of the matrix. For Queller and Goodnight's R, parent–offspring / full siblings = 0.50, 99% CI = 0.492–0.508, and half siblings = 0.25, 99% CI = 0.247–0.253). Red: full siblings, green: half siblings, blue: parent–offspring. Males are shown in blue (light blue: juvenile, dark blue: adult). Females are shown in pink (light pink: juvenile, dark pink: adult).

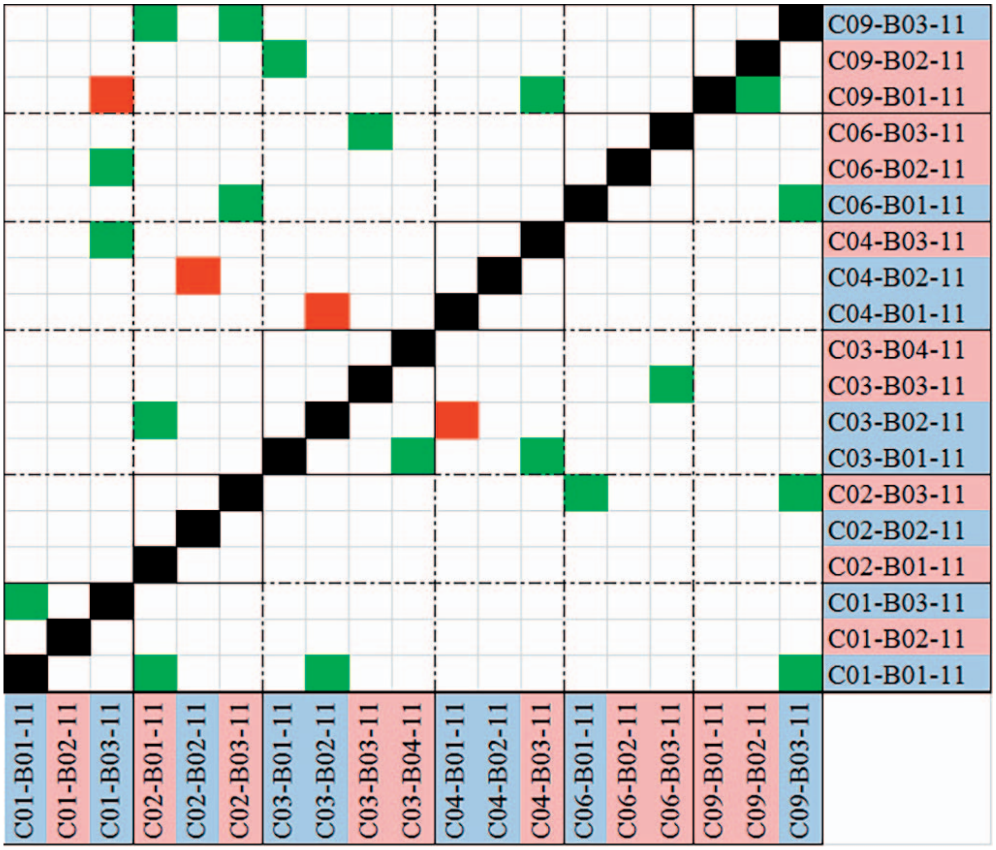

Fig. 6. Covey genetic relatedness for northern bobwhite (*Colinus virginianus*) within 2011–2012, South Texas. Probability of relatedness $\geq$0.99 from COLONY v. 2.0.4.5 (Wang 2004) is shown in the lower right of the matrix. Queller and Goodnight's *R* relatedness is shown above in the upper left of the matrix. For Queller and Goodnight's *R*, parent–offspring / full siblings $=$ 0.50, 99% CI $=$ 0.492–0.508, and half siblings $=$ 0.25, 99% CI $=$ 0.247–0.253). Red: full siblings, green: half siblings. Males are shown in blue, and females are shown in pink.

Faircloth (2008). Faircloth (2008) found evidence of extra-pair fertilizations to result in 1.8 ± 0.4 and 1.4 ± 0.6 chicks/wild and incubated broods, respectively, and extra pair fertilization rates of 10–20%/brood.

Genetic markers have revealed that promiscuity and extra-pair fertilizations are common in avian taxa (Griffith et al. 2002), including socially monogamous species (Carvalho et al. 2006, Ballenger et al. 2009). However, marker-based estimates of relatedness are not precise and may be error-prone or biased if assumptions are not met (DeWoody 2005, Jones and Wang 2010). Nevertheless, multiple methods used here produced similar results and it appears that the most likely explanation is promiscuous mating. An estimate of the extent and frequency of promiscuous mating would require genotyping the presumed parents and all chicks from each northern bobwhite nest.

Male and Female Relatedness

We did not expect to find a difference in male and female relatedness within the coveys. Average male relatedness (0.13) was at the level of first cousins (expected $R = 0.125$). Female relatedness within coveys (0.01) was essentially 0, close to the average relatedness of females (–0.02) and males (–0.007) among coveys (Fig. 4). This suggests that for families that stay together into the winter covey, the males either are staying closer to home than females or that male survival until the fall hunting may be slightly greater than female survival.

The disparity in relatedness for males and females is not readily apparent from studies of northern bobwhite movements. Both sexes may move similar distances at local scales (Stoddard 1931; Miller et al. 2017). Data from the Encino Division of the King Ranch, which is approximately 65 km southeast of our study area, indicates that males had longer average daily movements than adult females but only slightly longer than juvenile females. Maximum distance moved was shortest in adult females and longest for juvenile males (Miller et al. 2017; Fig. 1). Maximum distance moved was different among seasons for males and females. Adult males moved farther (583 m ± 121 SE) than juvenile males (531 m ± 115 SE), juvenile females (425 m ± 36 SE), and adult females (418 m ± 62 SE, Miller et al. 2017).

Data submitted to the South Texas Quail Associates Program (L. A. Brennan, Caesar Kleberg Wildlife Research Institute, unpublished data) shows that winter harvest male:female ratios from the study area ranged from 1.03 to 1.24, 2008–2013. The male:female ratio (~1 : 1) seems largely unaffected by annual rainfall, unlike juvenile:adult ratios, which are strongly affected by rainfall from April through August. It would seem the high degree of relatedness in males at the study area is not due to a skewed sex ratio in the winter but may be due to dispersal by females in the families. Tri et al. (2013) found a strong correlation between harvest juvenile:adult ratios and preceding summer rainfall totals but no correlation of male:female ratios to rainfall. This supports Lehmann's (1984:45) findings that winter coveys tended to have a fairly even ratio of males to females, regardless of weather.

This study provides a snapshot of covey relatedness in a defined area over a short time period. Analysis of entire coveys through live-trapping might give a more definitive overall distribution of siblings and, particularly after dry summers, might provide valuable insights into the mechanisms that maintain genetic diversity during periods of low census numbers. Further investigation of full:half sib relationships may require genotyping a subsample of these birds with a more extensive panel of markers and sampling stratified to areas of high northern bobwhite density and hunting pressure and areas of low density and low hunting pressure.

MANAGEMENT IMPLICATIONS

Multiple mating, the joining of larger social groups, and the fall shuffle may all play a role in maintaining genetic diversity for northern bobwhite populations. Northern bobwhite individuals appear to be moving among coveys enough to sufficiently disperse related individuals into other groups. This shuffling of genes may offset the "bust" years when populations drop drastically. Additionally, some gene flow among pastures and nearby ranches may be driven by the few northern bobwhites that move relatively longer distances (≥ 1 km). Populations isolated by distance may rely on these short distance movements, covey dynamics, and breeding strategies to sustain genetic diversity within their population. Further studies incorporating parentage analyses, movements, and covey dynamics will help biologists understand how this hunting may impact the genetic diversity of northern bobwhites.

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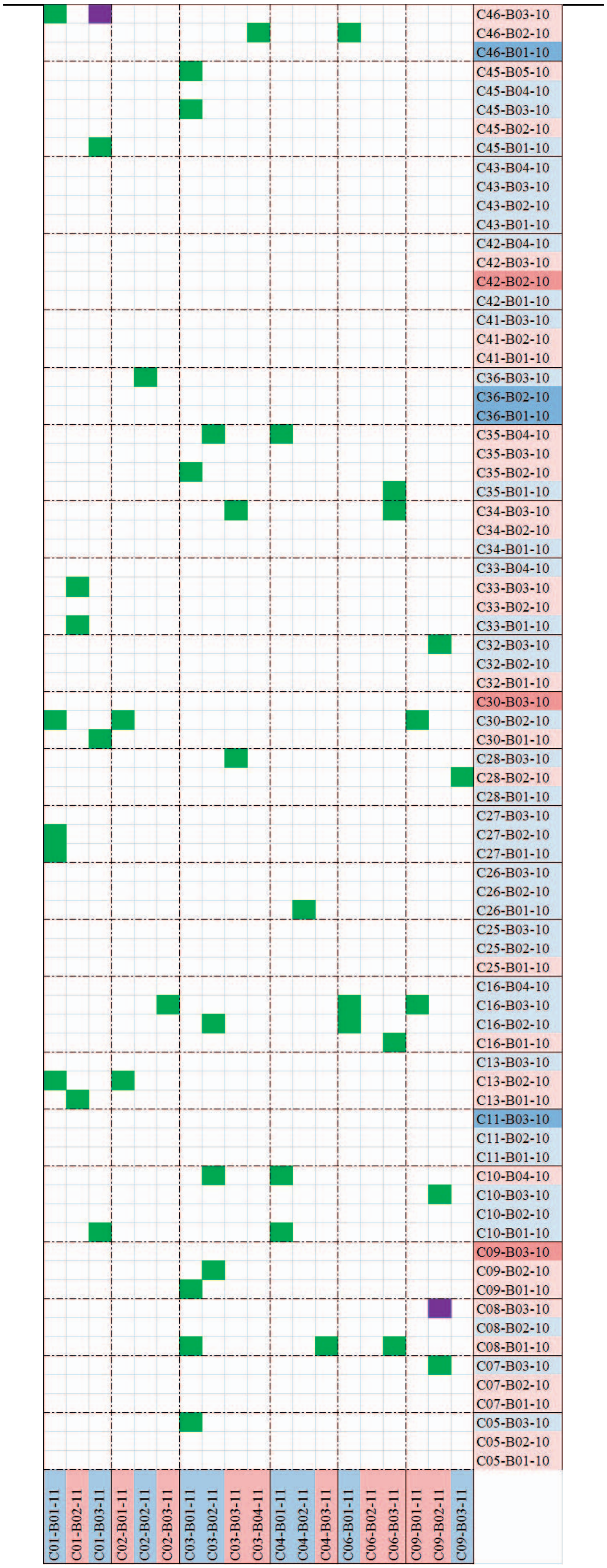

Fig. 7. Covey genetic relatedness for northern bobwhite (*Colinus virginianus*) among years. Probability of relatedness ≥ 0.99, from COLONY v. 2.0.4.5 (Wang 2004). Green: half siblings, purple: full siblings or parent–offspring (either the adult harvested in 2011–2012 was the parent to the young harvested in 2010–2011 or the birds are full siblings harvested in 2 separate years). Males are shown in blue (light blue: juvenile, dark blue: adult). Females are shown in pink (light pink: juvenile, dark pink: adult).

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EFFECT OF TEMPERATURE AND WIND ON METABOLISM OF NORTHERN BOBWHITE IN WINTER

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) are widely distributed across more than half of the United States, and extending into Canada and Mexico. Within this distribution they tolerate a wide range of climatic conditions and thermal stress. Annual variation in weather can produce dramatic short-term population fluctuations, particularly in the northern portion of the distribution. To better understand effects of thermal stress on energy requirements of bobwhite, we measured roosting metabolic response to cold stress and wind speed using open respirometry in a closed-circuit wind tunnel. Oxygen consumption was measured for 8 winter-acclimated captive bobwhites at each of 8 temperatures (–15°, –10°, –5°, 0°, 5°, 10°, 20°, and 30° C) at free convection and at 3 wind speeds (0, 1, and 2 m/sec) at –15° and 0° C. Over the range of body mass we measured (201.5 ± 1.3 g, $n = 64$), metabolic rate varied with body mass ($P < 0.001$) but did not differ between sexes ($P = 0.187$). Mean standard metabolic rate ($V0_2$) was 3.4 ± 0.11 mL O_2/minute/bird (0.0171 ± 0.0004 mL O_2/min/g) or 1.14 ± 0.04 W/bird. Below a lower critical temperature of 24.1° C, metabolic rate was linearly related to operative temperature (T_e)($V0_2 = 7.187 - 0.1568[T_e]$; $r^2 = 0.86$, $P < 0.001$). Metabolic rate (M–E) was linearly related to wind speed (WS) at –15° C ($V0_2 = 9.741 + 0.4609[WS]$; $r^2 = 0.99$, $P = 0.001$) and 0° C ($V0_2 = 6.713 + 0.4609[WS]$; $r^2 = 0.99$, $P = 0.001$). We discuss implications of these energy expenditures in the context of current research and management.

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Key words: *Colinus virginianus,* metabolism, northern bobwhite, operative temperature, roosting, thermoregulation

Northern bobwhite (*Colinus virginianus;* hereafter, bobwhite) are widely distributed from Florida to Canada and west to South Dakota and Mexico. Within this distribution they tolerate a wide range of climatic conditions and thermal stress, ranging from near-lethal heat loads at southern latitudes (Guthery et al. 2001) to acute cold stress at northern latitudes (Swanson and Weinacht 1997). Within the geographic distribution determined by long-term climatic and habitat conditions, annual weather variation can produce dramatic short-term population fluctuations, particularly in the northern portion of the distribution (Roseberry and Klimstra 1984). Survival during winter has been identified as the most important vital rate in central and northern parts of the species' distribution (Petersen et al. 2000, Folk et al. 2007, Sandercock et al. 2008, Gates et al. 2012). During winter, bobwhites at northern latitudes experience low ambient temperatures that may constrain space use (Tanner et al. 2017) and produce higher thermoregulatory costs during a period of declining food availability that is compounded by prolonged snow and ice cover that limit access to energy in food. Although direct mortality of bobwhites associated with winter weather is a minor component of total annual mortality (Roseberry and Klimstra 1984:60, Burger et al. 1995), the combination of low temperatures, deep or prolonged snow cover, and high winds can cause direct mortality (Errington 1939; Stanford 1972; Roseberry 1964; Roseberry and Klimstra 1972, 1984; Burger et al. 1995; Chavarria et al. 2012; Janke and Gates 2012; Janke et al. 2017) and deleterious

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indirect effects on populations. For example, reduced physiological fitness could occur, including increased susceptibility to toxins (Maguire and Williams 1987); and negative energy balance could reduce body condition, potentially delaying reproduction or predisposing quail to starvation or depredation.

Bobwhite respond to thermal stress through selection of habitat with a favorable microclimate (Roseberry 1964, Hiller and Guthery 2005, Tanner et al. 2017), adjusting duration of foraging activity (Guthery 2002), huddling (Case 1973), increasing metabolic heat production (Case 1973, Case and Robel 1974, Spiers et al. 1983, Swanson and Weinacht 1997), metabolizing lipid stores (Koerth and Guthery 1987, Guthery 2002), and as a last resort, catabolizing muscle mass. Unlike some bird species, bobwhite exhibit little seasonal adjustment in basal metabolic rate or insulation and core temperature is independent across a wide range of ambient temperature (Swanson and Weinacht 1997). Physiologically, bobwhite respond to acute cold stress primarily through adjustment in metabolic heat production and devote a large percentage (60–70%) of their winter energy expenditures to thermoregulation (Swanson and Weinacht 1997, Guthery 2002).

Thermoregulation in bobwhite has been the focus of a small number of studies examining both cold and heat stress. Case (1973) estimated energy intake, excretory energy, and existence energy of bobwhite under a 10 light : 14 dark photoperiod at a range of temperatures from 5° to 35° C and described behavioral (huddling) and energetic responses of bobwhite to cold stress. Case and Robel (1974) reported empirical relationships between existence energy and temperature for nonlaying females and males at temperatures from 5° to 35° C. Spiers et al. (1983) used indirect respirometry to measure evaporative heat loss, O_2 consumption, CO_2 production, and body temperature of bobwhite at 10–35° C, in 5° increments. Swanson and Weinacht (1997) used indirect respirometry to measure basal metabolic rate (BMR), metabolic response to temperature (–10° to 30° C), and maximal capacity for thermogenesis during diurnal and nocturnal periods in both summer and winter. However, all of these studies were conducted under free convective conditions. Whereas the effects of temperature on metabolic rates of birds is well-understood, the effects of forced convection on metabolic heat loss have been measured for relatively few species, but include neonatal mallards (*Anas platyrhynchos;* Bakken et al. 1999), verdin (*Auriparus flaviceps;* Wolf and Walsberg 1996), white-crowned sparrow (*Zonotrichia leucophrys;* Wolf et al. 2000), Gambel's quail (*Callipepla gambelii;* Goldstein 1983), ruffed grouse (*Bonasa umbellus;* Thompson and Fritzell 1988), and greater sage grouse (*Centrocercus urophasianus;* Sherfy and Pekins 1995), among others. Simultaneous effects of wind and temperature on bobwhite thermoregulation have not been measured.

Bobwhites can mitigate effects of thermal stress through selection of microclimates that produce energetically more favorable standard operative temperatures (T_{es}; Guthery et al. 2005, Hiller and Guthery 2005, Tanner et al. 2017). Microhabitats alter heat balance of individuals through effects of vegetation structure and substrate on radiant, conductive, and convective heat gain or loss. More specifically, during periods of cold stress, reflective and structural properties of roosting vegetation may increase T_{es} and reduce energy requirements by reducing radiant heat flow, conductive heat loss to soil surface, wind speed, and heat loss to forced convection. Empirical estimates of functional relationships between energy costs and temperature across a range of convective conditions would inform our understanding of the adaptive significance of microhabitat selection. Toward this end, we report on the effects of forced convection and temperature on the roosting metabolic heat production of winter-acclimated northern bobwhite.

METHODS

We acquired 8 bobwhites (4 M and 4 F) from a central Missouri commercial quail farm in December 1991. All bobwhites were 8–10 months old and 173–222 g ($\bar{x} = 201.5$, SE = 1.3 g) during the course of the experiment. We housed bobwhites colonially at ambient temperature in an open-air, covered pen at the Charles C. Green Wildlife Area 14.4 km south of Columbia, Missouri, USA. Birds were held on concrete floor with pine shavings litter. We provided bobwhites ad libitum water and commercial (Purina®; Purina Mills, LLC, Gray Summit, MO, USA) game bird feed. We conducted metabolic trials between 6 January and 9 March 1992. All birds were winter-acclimated at the time of trials. Mean monthly temperatures for Columbia, Missouri, during December 1991, January 1992, and February 1992 were 2.8°, 1.7°, and 4.4° C, respectively. Bobwhites were held at ambient winter photo periods without artificial light, and we conducted all trials during the dark portion of the diel cycle between 1900 and 0600 hours.

We estimated metabolic heat production using open circuit respirometry (Withers 1977) in a closed-circuit wind tunnel (Bakken et al. 1989). We measured oxygen concentration using an Applied Electrochemistry S-3A/1 oxygen analyzer with an R-1 flow control (Applied Electrochemistry, Inc., Sunnydale, CA, USA). Measurements of oxygen consumption at free convection used a 7.3-L (14.6 × 27.9 × 17.8 cm) rectangular chamber fabricated from galvanized sheet metal. Measurements under forced convection were in a 93.5-L dual-return, recirculating wind tunnel modeled after Bakken et al. (1989) and fabricated from galvanized sheet metal. The surfaces within the free-convection chamber and wind tunnel were coated with a nonhygroscopic, flat black paint. Within the wind tunnel, 2 stainless-steel wire-mesh screens confined birds within a 4.3-L chamber. We generated wind with a 25.4-cm-diameter × 20.3-cm blower wheel powered by a one-quarter horsepower electric motor regulated by a proportional controller. We regulated wind speed within the test chamber by varying voltage to the motor and measured wind speed at bird-level with a hot-wire anemometer. Stainless steel mesh screens ($n = 2$) in each of the 2 return chambers reduced turbulence and enhanced laminar flow characteristics in the test chamber. We did not measure uniformity of airflow within the test chamber; however, based on similar design, it was likely comparable to the ±5% reported by Bakken et al. (1989). We regulated temperature in the free convection chamber and wind tunnel by nesting the chambers within a 651-L chest freezer. The freezer was modified to accommodate the blower motor shaft penetrating the end wall with the fan motor and controller outside the freezer. During experimental trials, mean deviation of air temperature in the chamber relative to desired set temperature was –0.1° C (SD = 0.9). Wall temperature differed from air temperature by <0.5° C; consequently, T_a approximated T_e.

We measured metabolic heat production (VO_2 measured in mL O_2 per minute) for each of the 8 birds at each of 8 temperatures (–15°, –10°, –5°, 0°, 5°, 10°, 20°, 30° C) under free convection. Additionally, we measured metabolic heat production for each of the 8 birds at each of 6 combinations of 3 wind speeds (0, 1, 2 m/sec) and 2 temperatures (–15° and 0° C). We measured metabolic heat production under free convection during nocturnal roosting between 6 January and 9 March 1992. Metabolic measurements under forced convection were taken between 6 January and 4 March 1992. We generated a random order for individual bird, wind, and temperature combinations and conducted 1–3 trials/night. Individual birds experienced only 1 wind–temperature combination per night. We conducted nocturnal trials between 1900 and 0600 hours. At noon the day of the trial, we removed selected individuals from colony pens and confined them in a small cage to restrict access to food a minimum of 7 hours before the trial so that birds were in a postabsorptive state during the trials. Immediately prior to trials, we restrained birds in a nylon stocking and weighed them to 0.1 g on a precision balance. We placed birds unrestrained within the chamber on a wire mesh grate. We captured fecal droppings in a tray of mineral oil beneath the wire grate. Visual observations through a door in the top of the chamber confirmed that birds were resting during trials. We allowed birds to adjust to experimental temperature and convective conditions for 60 minutes prior to measurement of oxygen consumption. This equilibration period was adequate to allow VO_2 to achieve steady-state conditions.

Dry, CO_2-free room air was drawn through the chamber at 1,000–2,500 mL/minute and regulated with a Cole-Parmer (Vernon Hills, IL, USA) precision rotameter. A sample of dry, CO_2-free outflow chamber air was drawn through the S-3A Oxygen analyzer at 100 mL/minute and pO_2 continuously analyzed. We recorded fractional concentration of O_2 at 5-minute intervals and averaged over a 40-minute trial that followed the 60-minute acclimation–equilibration period. We calculated oxygen consumption using Withers (1977) equation 4a for dry, CO_2-free air entering the chamber and the oxygen analyzer (e.g., H_2O and CO_2 absorbents upstream of flowmeter and O_2 sensor). For calculations of metabolic heat production from VO_2, we assumed a respiratory quotient of 0.8 (Spiers et al. 1983) and 4.8 calories generated for each milliliter oxygen consumed (Rasmussen and Brander 1973). We express thermoregulatory responses of bobwhite in conventional units of oxygen consumption and watts (VO_2/min/bird, VO_2/min/g, W/bird, W/m^2). We estimated surface area from body mass using the equation for galliforms from Leighton et al. (1966) as cited in equation 1 of Spiers et al. (1983). We calculated total thermal conductance (° C measured in W/m^2/° C) according to Calder and King (1974) as illustrated in equation 3 in Spiers et al. (1983). We calculated dry thermal conductance (C_d measured in W/m^2/° C) following Spiers et al. (1983) equation 4.

We tested effects of sex and body mass on VO_2 and C_d under free convection across the range of T_e using a repeated-measures, mixed-model analysis of covariance with VO_2 as response, sex and T_e as categorical fixed effects, and body mass as a continuous covariate in PROC MIXED, SAS 9.4 (SAS 2002). To account for the repeated nature of the measurements of VO_2 on the 8 individual birds at each of the 8 temperatures, we included BIRD ID as a random effect using SUBJECT = BIRD ID and REPEATED = T_e options. In our mixed-model analysis we considered 4 alternative covariance structures (variance components, first-order autoregressive, compound symmetry, and heterogeneous compound symmetry) and selected heterogeneous compound symmetry based on lowest Akaike Information Criterion and Chi-square model-fit statistics.

Based on work by Case and Robel (1974), Spiers et al. (1983), and Swanson and Weinacht (1997), we anticipated that the lower critical temperature (T_{lc}) was somewhere below, and the upper critical temperature (T_{uc}) somewhere above, 30° C. Assuming that this value was within the thermoneutral zone (TNZ), we estimated standard metabolic rate (SMR) from measurements of VO_2 at 30° C under free convection. We modeled VO_2 below the TNZ as a function of temperature with simple linear regression using PROC REG in SAS (SAS 2002). We estimated T_{lc} for winter-acclimated bobwhite under free convection as the intersection between the regression line of VO_2 on temperature and a horizontal line through the mean VO_2 at 30° C. We modeled effects of wind on VO_2 at –15° and 0° C with linear regression using PROC REG in SAS 9.4 (SAS 2002). We tested for differences in slope and intercept for the 2 temperatures using a dummy regression model with VO_2 as response; wind speed as a continuous variable (0, 1, 2 m/sec); T_e (0° and –15° C) as a dummy variable coded 0 and 1, respectively; and the interaction WIND × T_e. The interaction between wind speed and T_e indicator variable was not significant ($t_1 = 1.05$, $P = 0.40$), indicating that the slopes of the regression lines for 0° and –15° C did not differ. We modeled common slopes but different intercepts using a reduced model with VO_2 as response, wind speed as a continuous variable, and T_e as a dummy variable (i.e., leaving out the interaction of WIND × T_e). Estimates of metabolic response are reported in the results as $\bar{x}$ ± standard error (SE).

We conducted bird husbandry, handling, and experimental trials in accordance with guidelines in the American Ornithologists Union Report of Committee on the Use of Wild Birds in Research (American Ornithologists Union 1988) and consistent with those of the

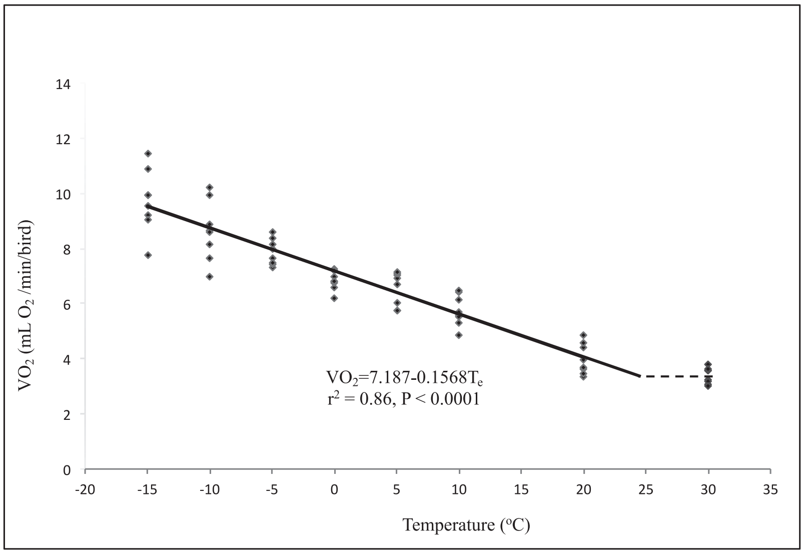

Fig. 1. Effect of operative temperature ($T_{e)}$ on metabolic heat production (VO_2) of northern bobwhite below the lower critical temperature ($n = 64$), from tests conducted on captive birds in Columbia, Missouri, USA, during 6 January-9 March, 1992.

University of Missouri Institutional Animal Care and Use Committee.

RESULTS

Standard metabolic rate of bobwhite, measured at $T_e = 30°$ C, was 3.4 ± 0.11 mL O_2/minute/bird or 1.14 ± 0.04 W/bird for a bird of mean weight 198.7 g (Table 1). Mass-specific SMR was 0.0171 ± 0.0004 mL O_2/minute/g. Surface-area–specific SMR was $41.9 + 1.1$ W/m^2. Over the range of body mass of birds used in this study ($\bar{x} = 201.5 \pm 1.3$ g, $n = 64$), metabolic rate was influenced by body mass ($F_{1,48} = 25.85$, $P < 0.001$) but did not differ between males ($\bar{x} = 6.68 \pm 0.104$ mL O_2/min/bird) and females ($\bar{x} = 6.54 \pm 0.104$ mL O_2/min/bird). VO_2 increased by 0.024 mL O_2/minute/bird for each 1-g increase in body mass. Outside the thermoneutral zone, BMR was negatively related to operative temperature ($VO_{2\ (mL/min/bird)} = 7.187 - 0.1568 \times T_e$, $r^2 = 0.86$, $P < 0.001$; or $VO_{2\ (mL/g/hr)} = 2.139 - 0.0470 \times T_e$, $r^2 = 0.86$, $P < 0.001$; Fig. 1). The mean lower critical temperature for bobwhite was estimated as 24.1° C. Metabolic rate (M–E) was linearly related to wind speed (WS) at –15° C ($V0_2 = 9.741 + 0.4609 \times WS$, $r^2 = 0.98$, $P = 0.001$) and at 0° C ($V0_2 = 6.713 + 0.4609 \times WS$, $r^2 = 0.98$, $P = 0.001$; Fig. 2). Dry thermal conductance (C_d) differed across operative temperatures (Fig. 3; $F_{7,48} = 30.39$, $P < 0.001$). Dry thermal conductance at 30° C was greater than at all other operative temperatures but C_d did not differ among operative temperatures below the lower critical temperature ($P > 0.05$).

DISCUSSION

Our findings represent 1 of just 3 experimental studies that directly measure the metabolic heat production of bobwhite within and below the thermoneutral zone and the only estimate of effect of wind speed on roosting metabolism. Our estimates of standard metabolic rate are within the range of values previously reported but we were able to more specifically estimate the lower critical temperature and the linear relationship between metabolic heat production and temperature below the lower critical temperature. The observed standard metabolic rate of 3.4

Table 1. Mean (SE) body mass, metabolic heat production measured as VO_2 (mL O_2/min/bird), VO_2/g (mL O_2/min/g), W (watts per bird), W/m^2 (watts/m^2); thermal conductance, C (W/m^2/° C); and dry thermal conductance C_d (W/m^2/° C) for winter-acclimated, nocturnal roosting northern bobwhite across operative temperatures (T_e) from –15° to 30° C under free convection. Data derived from tests conducted on captive birds in Columbia, Missouri, USA, during 6 January-9 March, 1992.

T_e	*n*	Mass (g)	VO_2	VO_2/g	W	W/m^2	C	C_d
−15	8	200.4 (4.9)	9.74 (0.40)	0.0487 (0.0019)	3.27 (0.13)	119.4 (4.7)	2.13 (0.08)	2.11 (0.08)
−10	8	203.8 (3.4)	8.67 (0.38)	0.0426 (0.0021)	2.90 (0.13)	104.9 (5.0)	2.05 (0.10)	2.03 (0.10)
−5	8	200.0 (4.1)	7.89 (0.17)	0.0395 (0.0010)	2.64 (0.06)	96.9 (2.3)	2.10 (0.05)	2.06 (0.05)
0	8	201.5 (3.2)	6.86 (0.12)	0.0340 (0.0003)	2.23 (0.04)	83.6 (0.8)	2.03 (0.02)	1.98 (0.02)
5	8	204.9 (4.4)	6.56 (0.22)	0.0320 (0.0009)	2.20 (0.07)	79.0 (2.2)	2.18 (0.06)	2.11 (0.06)
10	8	201.4 (3.7)	5.78 (0.20)	0.0287 (0.0009)	1.94 (0.07)	70.5 (2.2)	2.26 (0.07)	2.15 (0.07)
20	8	201.4 (3.7)	4.02 (0.20)	0.0200 (0.0010)	1.35 (0.07)	49.1 (2.5)	2.32 (0.12)	2.09 (0.11)
30	8	198.7 (3.9)	3.40 (0.11)	0.0171 (0.0004)	1.14 (0.04)	41.9 (1.1)	3.74 (0.10)	2.99 (0.08)

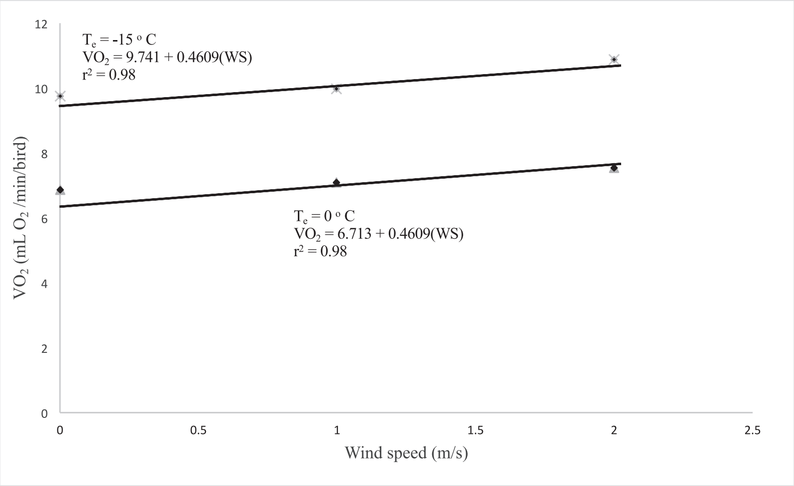

Fig. 2. Effect of forced convection on mean metabolic heat production of northern bobwhite at operative temperature (T_e) of –15° C ($n = 3$), $P < 0.001$) and 0° C ($n = 3$, $P < 0.001$), from tests conducted on captive birds in Columbia, Missouri, USA, during 9 January-4 March, 1992. Error bars are ± 1 standard error (SE).

mL O_2/minute/bird converted to kilocalories and extrapolated to a 24-hour period (23.50 kcal/bird/day) was 16% less than the 28.06 kcal/bird/day predicted from allometric equations for a 198.7-g bird (Zar 1969) and 8% less than existence metabolism (25.56 kcal/bird/day) reported by Case and Robel (1974) for bobwhite at 30° C and 10-hour photoperiod. Similarly, Guthery (2002:13) used equations derived from Case and Robel (1974) to estimate daily energy requirements of bobwhite, adjusted for active and inactive periods, during winter under a 10-hour day length at 25° C. The daily energy requirement of 117.1 kJ/day estimated by Guthery (2002) was approximately 16% greater than the 98.37kJ/day/bird predicted from our measurement of VO_2 at 30° C. Insofar as SMR in our study was measured only during the inactive period and both the Case and Robel (1974) study and Guthery (2002) included both active and inactive periods, a slightly lower value is not unexpected. Only 2 studies—Spiers et al. (1983) and Swanson and Weinacht (1997)—have measured metabolic heat production of bobwhites using indirect calorimetry. Spiers et al. (1983) reported metabolic heat production of bobwhite at 30° C as 47.76 W/m^2 or 12% greater than the 41.9 W/m^2 that we observed. However, the mass-specific SMR (1.03 + 0.03 mL O_2/g/hr) that we observed was only 3% less than that (1.06 mL O_2/g/hr) reported by Spiers et al. (1983). The mean SMR of 3.4 ± 0.11 mL O_2/minute/bird observed during our study was approximately 9.6% less than the 3.76 mL O_2/minute/bird BMR reported by Swanson and Weinacht (1997) for winter-acclimated bobwhites. Winter-acclimated birds used in Swanson and Weinacht (1997) had approximately 10% greater mean body mass

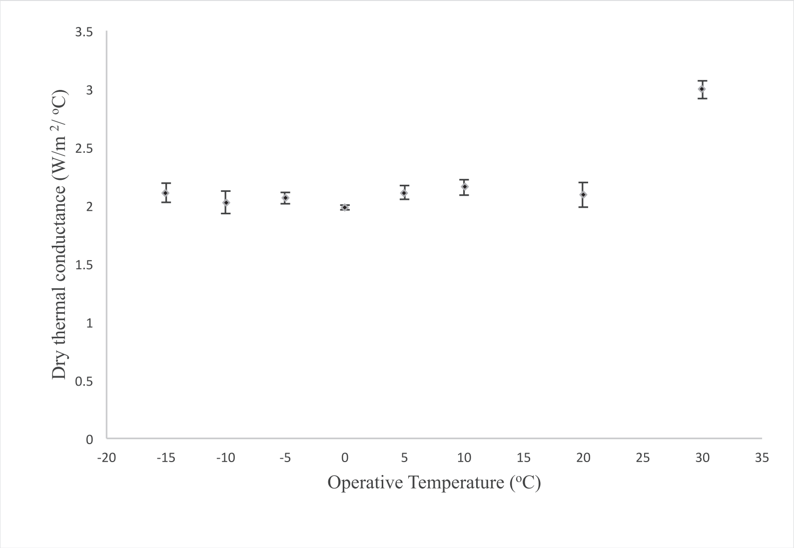

Fig. 3. Dry thermal conductance of northern bobwhite ($n = 8$) at operative temperatures (T_e) of –15–30° C, from tests conducted on captive birds in a Columbia, Missouri, USA, during ###–###. Error bars are ± 1 standard error (SE).

(228 ± 36 g) and the mass-specific BMR observed in our study (1.03 + 0.03 mL O_2/g/hr) was similar to that reported in their study (1.01 + 0.11 mL O_2/g/hr).

Hiller and Guthery (2005) estimated that bobwhites exhibited heat-seeking behavior at T_e <26.7° C. Case (1973) speculated that the lower critical temperature for bobwhite was between 10° and 20° C. Spiers et al. (1983) did not specifically determine T_{lc} but speculated it might be between 30° and 35° C. Our estimate of T_{lc} (24.1° C) was intermediate between the values reported by Swanson and Weinacht (1997) for winter- (22.4° C) and summer- (25.5° C) acclimated bobwhite and similar to the 26.7° C determined by Hiller and Guthery (2005). Below the thermoneutral zone, metabolic response of bobwhite increased linearly with decreasing T_e. The slope of the relationship between mass-specific metabolic rate and T_e (–0.0470 mL O_2/g/hr) was nearly identical to that reported for winter nocturnal bobwhite (–0.05 mL O_2/g/hr) in Swanson and Wienacht (1997) and similar to that (–0.0717 mL O_2/g/hr) reported in Spiers et al. (1983).

Dry thermal conductance within the thermoneutral zone (2.99 ± 0.08 W/m^2/° C or 0.07 ± 0.002 mL O_2/g/hr) was approximately 50% greater than that observed below the T_{lc} (2.03–2.32 W/m^2/° C or 0.048–0.051 mL O_2/g/hr/° C). Dry thermal conductance below the thermoneutral zone was relatively invariant, indicating that below the T_{lc} bobwhites had adopted all available behavioral and postural means of energy conservation. Our observed C_d below the T_{lc} was less than the 3.18–3.35 W/m^2/° C reported by Spiers et al. (1983) but similar to the winter nocturnal rate (0.058 ± 0.007 mL O_2/g/hr/° C) reported by Swanson and Weinacht (1997).

Metabolic rate of bobwhites increased linearly with wind speed at both –15° C and 0° C and the slopes of the relationship between VO_2 and wind speed did not differ between operative temperatures. Although avian metabolic rate has commonly been reported to vary with the square root of wind speed (e.g., Thompson and Fritzell 1988), Goldstein (1983) reported that metabolic rate of Gambel's quail increased linearly with wind speed. Goldstein (1983) reported that the slope of the relationship between metabolic rate and wind speed varied across T_a with greater slope at lower temperatures. Thompson and Fritzell (1988) also reported that, for ruffed grouse, slopes differed between T_e. However, they observed the steepest slope at the higher temperature, opposite the pattern reported by Goldstein (1983). As Goldstein (1983) acknowledged, at temperatures below the thermoneutral zone, the difference between T_b and T_a (ΔT) creates the gradient that drives the rate of heat loss; and loss is greater at lower T_a, assuming constant T_b. Therefore, heat loss will increase to a greater degree across wind speeds at a lower temperature than higher (Goldstein 1983). Consequently, the slope of the relationship between metabolic heat production and wind speed should increase with ΔT (i.e., lower T_a). The failure to detect T_e-specific slopes in our study may have been, in part, a function of low power associated with the relatively small number of wind speeds examined ($n = 3/T_e$ vs. $n = 5/T_e$ in Goldstein 1983).

Across much of the bobwhite distribution, winter night-time temperatures commonly fall below –15° C and impose substantive thermoregulatory costs on bobwhites. At a temperature of –15° C with no wind, our predicted metabolic rate was 2.9 times greater than SMR. A wind speed of 2 m/second increased metabolic rate by an additional 9.5%. At temperatures below the TNZ, birds may respond to thermal stress by regulating metabolic heat production (Case 1973, Case and Robel 1974, Spiers et al. 1983, Swanson and Weinacht 1997), huddling (Case 1973), and selection of favorable microclimate (Roseberry 1964, Hiller and Guthery 2005, Tanner et al. 2017). Guthery et al. (2005) used thermal radiotransmitters to demonstrate that at ambient temperatures <16.2° C, roosting bobwhites experience standard operative temperatures greater than ambient air temperatures, meaning that roost sites and roosting behavior collectively improve the thermal environment for bobwhite, leading to energy conservation. The magnitude of this effective thermal increment was 8.6° C at an ambient air temperature of 0° C and increased with decreasing temperature (Guthery et al. 2005). Vegetation structure at roost sites that reduces wind speed will diminish heat loss from forced convection and microhabitat features that decrease convective, radiant, and conductive heat loss may improve energy balance. Tanner et al. (2017) concluded that lack of favorable microhabitats during severe winter weather can substantially limit distribution of individual bobwhite coveys. They found a significant reduction in usable space below –15° C and predicted that, during the lowest temperatures studied in northern Oklahoma, favorable microhabitats occurred on only 18.6% of the landscape. If microhabitat structure alters the radiative or convective environment, it will almost certainly affect T_{es}. As illustrated in our study, microhabitat structure that simply reduces wind speed at bird-level from 2 m/second to free convective conditions will result in nearly 10% reduction in thermoregulatory costs. Tanner et al. (2017) emphasized the fitness-reducing effect of winter conditions and cautioned that habitat measurements averaged across years or seasons will incorrectly identify critical habitat elements, and confound understanding of bobwhite energy conservation and predator avoidance. Our empirical estimates of functional relationships between energy costs and temperature across a range of convective conditions provide a basis for understanding the adaptive significance of bobwhite microhabitat selection.

MANAGEMENT IMPLICATIONS

Our finding of increased energy expenditures by bobwhites in response to low temperature and increasing wind speed reinforces the need by bobwhite managers to consider factors that provide a positive energy balance (i.e., more energy intake; for example, via high-energy seeds) and less energy loss (e.g., via habitat, less distance traveled within habitats, less harassment by hunters and dogs).

With few exceptions bobwhite populations are declining, more so on the northern fringe from Wisconsin to New Jersey, with bobwhites extirpated in Pennsylvania (McKenzie et al. 2015:46). Bobwhite management is closely scrutinized, with citizens simultaneously expecting very large populations for hunting, populations that are viable, and population restoration in areas of extirpation. In areas subject to severe winter, managers should thoughtfully consider energy balance of individual bobwhite.

As noted in this proceedings, there is considerable demand and need for translocation of bobwhites and among the uncertainties of this practice is the appropriateness for energy balance of moving smaller southern bobwhites to northern latitudes. Our finding of increased thermoregulatory energy expenditure adds emphasis to existing knowledge for bobwhites in this regard and reinforces the importance of considering ecological principles (i.e., Allen's and Bergmann's Rules). The bobwhites' relatively small size and high surface-area-to-volume ratio translates to size-specific energy capacity. Beyond generalizations, however, researchers should provide managers with bobwhite energy budgets for translocation destinations and data regarding the capacity of different-sized bobwhites to thrive energetically in those locations.

ACKNOWLEDGMENTS

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USING FIRST PASSAGE TIME ANALYSIS TO IDENTIFY FORAGING PATTERNS OF THE NORTHERN BOBWHITE

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ABSTRACT

Patterns in movement data can reveal important information relating environmental variables to behavioral mechanisms. First passage time analysis (hereafter; FPT) can be used to quantify the spatial and temporal variation in movements by identifying areas of restricted search behavior based on measuring residence time in an area. It is applicable in studies of foraging ecology and habitat selection because it can empirically quantify behavioral decisions without any *a priori* assumptions of habitat availability. Furthermore, FPT analysis is simple to implement and interpret; however, the technique has yet to be applied to the northern bobwhite (*Colinus virginianus*, hereafter bobwhite) because telemetry locations in short (e.g., 30 min) successive time intervals are needed. Our primary objective was to better understand patterns in foraging behavior of bobwhites as it relates to habitat use and improve management. Our secondary objective was to test the efficiency of using FPT analysis on telemetry data collected at different time intervals. Bobwhites were captured during the fall of 2013 and 2014 on a private plantation in South Carolina and fitted with very high frequency (VHF) transmitters ($n = 143$ and $n = 148$, respectively). We located coveys at 1 hour (2013) and 30 (2014) minute time intervals during daylight. Bobwhites concentrated their searching efforts to a few hours pre-dusk. Search efforts were proximal to supplemental food sources, with some intra-seasonal variation. Advances in global positioning system (GPS) technology will likely increase opportunities for collecting fine-scale movement data for bobwhites. Understanding techniques such as FPT analysis will enhance our knowledge of northern bobwhite ecology and management.

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Key words: behavior, *Colinus virginianus*, first passage time, foraging, habitat use, northern bobwhite

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COMPARING THE ACCURACY OF EGG CANDLING AND EGG FLOTATION TO ESTIMATE THE HATCHING DATE OF NORTHERN BOBWHITE CLUTCHES

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ABSTRACT

Floating and candling avian eggs to assess hatch dates has been used successfully to estimate hatch dates for wild bird clutches for decades. However, there is a dearth of information assessing the accuracy of these techniques to estimate northern bobwhite (*Colinus virginianus*) hatch dates. We captured and fitted a hen bobwhites with very high frequency transmitters during January and February of 2011–2012. We monitored each bird twice weekly until nesting was initiated. We searched for the nest while the hen was away from the nest (i.e., feeding) to reduce potential abandonment. We used egg floatation and egg candling methods to attempt to estimate wild northern bobwhite clutches during the 2011–2012 nesting seasons. We used a mini MagLite© (97 lumens; Mag Instrument, Inc., Ontario, CA, USA) with the glass lens removed so eggs would sit near the bulb to increase the illumination. We used a dark green 68-cm × 137-cm towel to cover the observer in the field to reduce the naturally occurring light, which might have reduced the visibility of the chick embryo. We based age of the eggs (no. of days since the start of incubation) on the embryo growth stage at the time of nest discovery. We conducted egg floatation at the same time as candling. We used a 100-mL glass beaker with 100-mL of ambient temperature tap water to completely submerge the egg to estimate hatch date. We based the flotation estimation age on the angle at which the egg floated in the water. We also conducted a controlled laboratory experiment using pen-raised quail eggs collected from the breeding colony at the Quail-Tech Alliance breeding facility in Lubbock, Texas. We placed 110 eggs in a commercial incubator that was maintained at 37° C with 55% humidity for the duration of the study. We used 3 novice observers to determine the impact of observer bias on the techniques of estimating hatch date. We placed random groups of eggs (i.e., 5–15 eggs at a time until 110 eggs were obtained) into the incubator at a staggered rate to increase variation in the study. We used the same field techniques for hatch date estimation in the controlled study. We first floated eggs during both controlled and field observations to reduce any potential bias that candling might have on the hatch date estimation (i.e., lack of embryo growth). During the controlled study observers examined the eggs individually. Using the average estimated hatch date (Julian date) as a predictor, we used linear regression to determine the accuracy of the candling and floating methods. We also used a linear regression to determine the accuracy of each estimation technique and observers. When candle and egg floating occurred in a field setting, both methods were found to overestimate the actual hatch date of the clutches discovered ($n = 47$; $R^2{}_2 = 0.993$, $P < 0.001$; estimated hatch days when using candle: $\bar{x} = 1.21 \pm 0.92$ days, floating: $\bar{x} = 0.89 \pm 0.97$ days). However, the mean difference between the candling and floatation was –0.38 days (SE = 1.07 days). Regression analysis suggests that candling and egg flotation are fairly accurate predictors of the actual hatch date for newly discovered bobwhite nests (candling: $\beta = 0.43$, $t = 3.75$, $P = 0.001$; floating: $\beta = 0.53$, $t = 4.79$, $P < 0.001$). Use of the candling method appears to be correct 43% of the time whereas egg floatation accurately predicted the estimated hatch date 53% of the time. Under controlled conditions, all 3 observers were new to both techniques of hatch date estimation and were all taught by the same instructor for each method. During the controlled test, we found that observers were highly variable. Two observers could predict the estimated hatch date by using the candling and egg flotation methods to a close estimation of the actual hatch date (floating [observer 1: $\beta = 0.23$, $t = 2.80$, $P = 0.006$ and observer 2: $\beta = 0.47$, $t = 5.52$, $P < 0.001$]; candling [observer 1: $\beta = 0.30$, $t = 4.00$,$P = 0.006$, observer 2: $\beta = 0.219$, $P < 0.01$]). Although observer 3 was unable to predict the estimated hatch date for both estimation methods (floating: $\beta = –0.001$, $t = –0.013$, $P = 0.684$; candling: $\beta = 0.043$, $t = 0.40$, $P = 0.990$). We also examined any potential abandonment or hatchability issues that might have risen while using candling or floating to estimate hatch dates for wild clutches. We found that 0.06% (5 of 80 nests) of hens abandoned their clutches during this study. Of the 5 nests that were abandoned zero were abandoned because of measurements obtained during the initial investigation of the nest site. All abandonments were due to either weather (i.e., summer hail), predators, or livestock. Viability and hatchability were unaffected for the remaining clutches that were measured during the field study. We found that candling and egg flotation are both viable methods for estimating hatch dates of bobwhite clutches during an initial measurement when a nest is discovered. When an entire clutch is measured accuracy can be within 1 day of the actual estimated hatch date (based on a 24-day incubation period). However, observers or researchers who will estimate hatch dates for clutches should be properly trained and allowed time to acclimate to the measuring techniques to potentially increase their accuracy at estimating hatch dates for northern bobwhite clutches.

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Key words: egg candling, egg floatation, *Colinus virginianus,* hatch date, linear regression, northern bobwhite

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GENETIC STRUCTURE OF NORTHERN BOBWHITE IN THE ROLLING PLAINS

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ABSTRACT

The recent declines in northern bobwhite quail populations in the Rolling Plains of Texas have raised concerns about habitat connectivity and gene flow. In addition, bobwhites have several life history traits that make them likely to display high levels of spatial genetic structure including low survival, high reproductive rates, and low dispersal rates. To determine if populations within the Rolling Plains have limited gene flow, we investigated the genetic structure of northern bobwhites within the ecoregion. Blood samples were collected at 16 ranches, encompassing 22 million acres, between February 2010 and April 2013. Bobwhites were also samples at a ranch in South Texas to serve as an outgroup. Samples ($n = 647$) were genotyped at 14 microsatellite loci that averaged 19.00 ± 5.07 alleles per loci. Global Fst indicated significant genetic structure ($p = 0.001$) between ranches with no isolation by distance signal ($p = 0.079$). Program STRUCTURE, however, indicated many ($n = 30$) overlapping subpopulations with no ranch constituting a single subpopulation and individuals from the outgroup ranch were included in 11 subpopulations. It appears that bobwhites within the Rolling Plains have few restrictions to gene flow and dispersal is not limited by the dominant habitat, xeric rangeland. These results suggest that populations in the Rolling Plains are not in danger of becoming isolated nor are bottlenecks present due to the recent decline.

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Key words: Gene flow, connectivity, population decline, Rolling Plains

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GEOGRAPHIC SURVEY OF *OXYSPIRURA PETROWI* AMONG WILD NORTHERN BOBWHITES IN THE UNITED STATES

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ABSTRACT

Eyeworms (*Oxyspirura petrowi*) are potentially associated with northern bobwhite (*Colinus virginianus*) declines. We examined hunter-donated bobwhites from the 2013–2015 hunting seasons in 9 states to document infection prevalence (% of bobwhites [of total n]) and intensity (mean no. of eyeworms ± SE). Four states harbored infected bobwhites: Texas (59.1% [$n = 110$], 15.6 ± 2.1), Oklahoma (52.1% [$n = 121$], 6.9 ± 1.2), Virginia (14.8% [$n = 27$], 2.5 ± 1.0), and Alabama (1.6% [$n = 61$], 2.0). Prevalence and intensity of eyeworms in the Texas Rolling Plains were greater ($P < 0.001$ and $P = 0.002$, respectively) than in any other area sampled. Based on our survey, eyeworms are locally prevalent and abundant in bobwhites from the Rolling Plains ecoregion, but virtually nonexistent in many areas that we surveyed.

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Key words: *Colinus virginianus,* eyeworm, northern bobwhite, *Oxyspirura petrowi,* Rolling Plains

The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) has experienced declining populations across its geographic range for ≥40 years with the ultimate cause of the decline attributed to habitat loss and fragmentation (Hernández and Guthery 2012, Sauer et al. 2014). However, bobwhites are also declining in areas where ample habitat remains (e.g., parts of TX and OK) suggesting that other factors may be involved in the quail decline (Dunham et al. 2014). Recently, researchers in Texas began to revisit parasitic infections in bobwhites to 1) update survey records from the late 1960s (Jackson and Green 1965, Jackson 1969), and 2) investigate parasitic infections as a potential factor in bobwhite population declines. A survey completed by Villarreal et al. (2016) in 2012 in Fisher County, Texas, found the eyeworm, *Oxyspirura petrowi,* to be common (57%) in bobwhites. This prompted further surveys to elucidate the geographic range of *O. petrowi* in wild bobwhites, particularly in areas where bobwhite populations have experienced significant decline.

Eyeworms are heteroxenous, indirect life-cycle nematodes that parasitize the orbital cavity, intraorbital glands, and nasal sinuses of ≥28 avian species in North America (Pence 1972, Dunham et al. 2014, Bruno et al. 2015; Fig. 1). The intermediate host for *O. petrowi* is unknown; however, Surinam cockroaches (*Pycnoscalus surinamensis*) are known intermediate hosts for *O. mansoni,* a similar eyeworm found in domestic chickens (Schwabe 1951). Kistler et al. (2016) successfully infected bobwhites with third-stage larvae via Plains lubber grasshoppers (*Brachystola magna*). However, lubbers are not a known food source for bobwhites. Thus, the intermediate host is still considered an unknown arthropod. Infected bobwhites may exhibit keratitis (i.e., scarring of the cornea) and other signs associated with inflammatory responses (Bruno et al. 2015). Histological results do not imply whether infection causes visual impairment or reduced fitness, but coupled with high prevalence, *O. petrowi* infections warrant further investigation.

After the initial survey by Villarreal et al. (2016; 2009–10), recent surveys from the Rolling Plains of Texas and Oklahoma documented *O. petrowi* prevalence ranging from 50% to 100% in bobwhites (Dunham et al. 2014, 2016; Villarreal et al. 2016). High prevalence in this region is consistent with results from surveys by Jackson and Green (1965) finding *O. petrowi* at 44% prevalence ($n = 605$). Outside of Texas, *O. petrowi* has been recorded in bobwhites from Louisiana (Palermo and Doster 1970) and Florida (Davidson et al. 1991), but at very low prevalence (<1%). These earlier accounts in the Southeast dismissed eyeworm infections as extremely rare and probably

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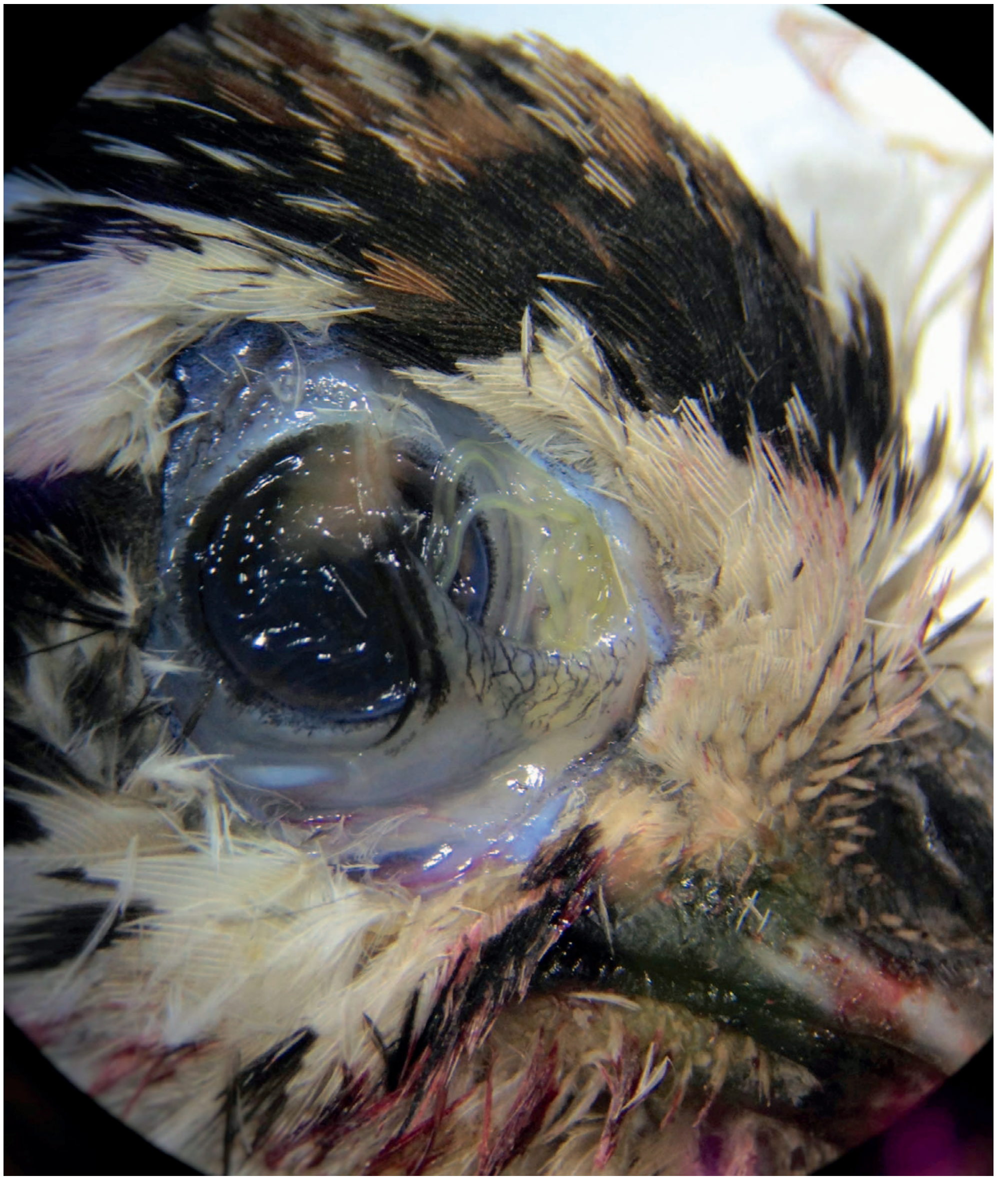

Fig. 1. Orbital cavity of a northern bobwhite (*Colinus virginianus*) infected with *Oxyspirura petrowi*. Nictitating membrane has been removed to reveal several eyeworms aggregated at the right lacrimal.

incidental in wild bobwhites (Kellogg and Calpin 1971, Kellogg and Doster 1972, Davidson et al. 1982). It is likely many earlier studies overlooked or dismissed the importance and presence of parasites in intraorbital glands (Peterson 2007, Dunham et al. 2014). Therefore, our objective was to thoroughly examine and opportunistically survey wild bobwhites from across the United States to determine geographic prevalence and intensity.

STUDY AREA

Heads of wild bobwhite and respective wing samples were collected via hunter-shot donations and miscellaneous submissions to the Rolling Plains Quail Research Ranch from agency biologists in 9 states and from hunters and landowners in Texas during January 2013–February 2016. Our sample ($n = 782$) consisted of birds submitted from Alabama, Georgia, Iowa, Kentucky, Louisiana, Missouri, Oklahoma, Texas, and Virginia.

METHODS

We instructed hunters to freeze all samples as soon as possible after death to prevent deterioration and possible emigration of the eyeworms. We thawed frozen samples in a refrigerator overnight before examination. Using curved forceps and dissecting scissors, we removed the outer eyelids before examining beneath the nictitating membrane. Although eyeworms are apparent to the naked eye, we used a stereo zoom microscope (7×–45×) and a 3 diopter (1.75×) magnifying lens with light-emitting-diode illumination to assure detection. After examining and removing any eyeworms residing beneath the nictitating membrane, we removed the eyes and separated the

Table 1. Prevalence (percent of hosts infected), mean intensity (average eyeworms per infected host), and mean abundance (average for total sample) of *Oxyspirura petrowi* from northern bobwhites (*Colinus virginianus*) sampled from wild, hunter-donated bobwhites harvested during the 2013–2015 hunting seasons across 9 states in the United states.

			Intensity		Abundance	
State	*n*	Prevalence no. (%)	$\bar{x} \pm$ SE	Range	$\bar{x} \pm$ SE	Total
AL	61	1 (2)	2 ± N/A	1–2	$<0.1 \pm <0.1$	2
GA	79	0	0	0	0	0
IA	56	0	0	0	0	0
KY	36	0	0	0	0	0
LA	25	0	0	0	0	0
MO	267	0	0	0	0	0
OK	121	63 (52)	6.9 ± 1.2	1–56	3.6 ± 0.7	433
VA	27	4 (15)	2.5 ± 1.0	1–5	0.4 ± 0.2	10
TX[a]	110	65 (59)	15.6 ± 2.1	1–79	9.2 ± 1.4	1,015

[a] Rolling Plains ecoregion (Gould 1975).

Harderian and lacrimal glands. We then dissected and examined the nasal sinuses. We fixed all eyeworms recovered for 10 minutes in glacial acetic acid before preserving them in a solution of 70% ethyl alcohol and 8% glycerol. Definitive identification was accomplished examining morphological characteristics described by Pence (1972) under a Leica EZ4D dissection microscope (Leica Microsystems, Wetzlar, Germany). We documented age (e.g., juvenile, adult) and sex of bobwhites.

We conducted Chi-square analysis using PROC FREQ in SAS 9.3 (SAS Institute Inc., Cary, NC, USA) to compare eyeworm prevalence between bobwhite age and sex classes by state. We tested for normality of eyeworm intensity using PROC UNIVARIATE. Data of eyeworm abundance and intensity were not normally distributed. Thus, we used PROC NPAR1WAY to compare mean intensity and mean abundance for bobwhite age and sex classes by state, determining significance at $P \leq 0.05$. Means are expressed as mean ± standard error (SE).

In an effort to standardize terminology, parasitological definitions presented herein follow Bush et al. (1997) where "prevalence" describes percent of infected individuals in a sample; "mean abundance" describes average number of eyeworms among all samples (i.e., infected and noninfected), and "average intensity" describes the average number of eyeworms within the subset of infected individuals only.

RESULTS

We examined the eyes, intraorbital glands, and sinuses of 782 wild bobwhite from 9 states: Alabama ($n = 61$), Georgia ($n = 79$), Iowa ($n = 56$), Kentucky ($n = 36$), Louisiana ($n = 25$), Missouri ($n = 267$), Oklahoma ($n = 121$), Virginia ($n = 27$), and Texas ($n = 110$; Table 1). In Texas, wings were not submitted with every head sample so not all bobwhite ages could be recorded ($n = 26$).

Four of the 9 states had bobwhites that hosted *O. petrowi*—Alabama, Oklahoma, Texas, and Virginia. Prevalence varied greatly among the 4 states from which eyeworms were identified. Only 1 adult male bobwhite from Alabama was infected with 2 eyeworms (1.6% prevalence) while Texas, Oklahoma, and Virginia had 59.1% ($n = 65$), 52.1% ($n = 63$), and 14.8% ($n = 4$) prevalence, respectively (Table 1). Average intensities were 15.6 ± 2.1 (95% CI = 13.5–17.7), 6.9 ± 1.2 (95% CI = 5.7–8.1), and 2.5 ± 1.0 for Texas, Oklahoma, and Virginia, respectively. Texas had a greater mean abundance (9.2 ± 1.4) of eyeworms than did Alabama ($0.1 < 0.1$), Oklahoma (3.6 ± 0.7), or Virginia (0.4 ± 0.2; $F = 24.6$, $P < 0.001$; Table 1).

Prevalence was similar between sexes for bobwhites from Oklahoma (Yates $\chi^2 = 0.48$, $P = 0.49$) and Texas (Yates $\chi^2 = 0.19$, $P = 0.68$). Pooling across Texas and Oklahoma, prevalence was also similar between sexes (Yates $\chi^2 = 0.83$, $P = 0.36$). Prevalence was similar between juvenile and adult bobwhites in Texas (Yates $\chi^2 = 2.13$, $P = 0.144$).

Mean intensity was similar between males and females in Texas ($P = 0.41$) and Oklahoma ($P = 0.43$). Pooled across Oklahoma and Texas, mean intensities were also similar ($P = 0.16$). Mean intensity between juveniles and adult bobwhites in Texas approached significance ($P = 0.06$) with adults ($n = 12$) having greater intensities (18.8 ± 5.1) than did juveniles (9.4 ± 2.3; $n = 27$).

DISCUSSION

The bobwhites from Texas and Oklahoma sampled in this study came from the Rolling Plains ecoregion located in the northwestern part of Texas extending into western Oklahoma (Gould 1975). Previous studies from areas surrounding this region have reported *O. petrowi* prevalence among bobwhites and other Galliformes ranging from 3% to 95% (Pence and Sell 1979; Pence et al. 1980, 1983; Robel et al. 2003). Eyeworms appear to be enzootic and prolific in this ecoregion since at least the early 1960s (Jackson and Green 1965, Jackson 1969). By contrast, bobwhites in the Rio Grande Plains of southern Texas are less parasitized by eyeworms. Olsen and Fedynich (2016) examined 244 bobwhites during 2012–2014 in the South Texas Plains ecoregion and reported considerably lower *O. petrowi* prevalence (9%) and intensity (4.9 ± 1.7) compared with our estimates from the Rolling Plains. This geographic difference within Texas warrants further investigation. Speculation of higher localized prevalence and intensities in the Rolling Plains could be attributed to intermediate host distribution and abundance, transmission rates (i.e., proportion of individuals that become infected from exposure to agent), or other undetermined factors. Evidence suggests that density-dependent, intermediate-host dynamics exists where parasite abundance is assumedly greater because of greater arthropod abundance and diversity, but this occurrence has not been quantified (Landgrebe et al. 2007).

Although our study did not find any significant differences by age, previous studies on bobwhites from Texas noted significantly higher prevalence and abundance of *O. petrowi* in adult bobwhites (Jackson and Green 1965; Dunham et al. 2014, 2016; Villarreal et al. 2016). Jackson and Green (1965) were the first to note eyeworm infections in wild bobwhites in the Rolling Plains of Texas with prevalence of 44% and intensity ranging from 1 to 30. Our data suggest similar prevalence and intensity to those reported by Jackson and Green (1965) and other recent accounts in the Rolling Plains (Dunham et al. 2014, 2016; Villarreal et al. 2016).

Oxyspirura petrowi has been reported previously in other Galliformes in states outside of Texas and Oklahoma. *Oxyspirura petrowi* was reported in <1% ($n = 203$) of ruffed grouse (*Bonasa umbellus*) in Minnesota (Erickson et al. 1949), 32% ($n = 149$) of sharp-tailed grouse (*Tympanuchus phasianellus*) and in greater prairie-chickens (*T. cupido;* Saunders 1935, Cram 1937) from Michigan. More notable infections of *O. petrowi* were found in 47% ($n = 57$) of ring-necked pheasants (*Phasianus colchicus*) in Nebraska (McClure 1949) and 95% ($n = 56$) of lesser prairie-chickens (*T. pallidicinctus*) in Kansas (Robel et al. 2003). Our findings would be complemented by examining bobwhites from Nebraska and Kansas where *O. petrowi* infections have been recorded at high prevalence in pheasants and prairie-chickens. This is the first study to report *O. petrowi* from bobwhites or any Galliformes in Alabama or Virginia.

It is important to distinguish what characteristics of parasitic infections cause disease. As such, we accept Wobeser's (1981) definition that a disease is "any impairment that interferes with or modifies the performance of normal functions, including responses to environmental factors such as nutrition, toxicants, and climate, infectious agents, inherent or congenital effects; or a combination of these factors." The effect of eyeworms on bobwhite physiology, behavior, and demographics (e.g., survival, reproduction) is currently being studied, but existing evidence for potential impacts on survival of bobwhites is speculative. Given that no data exist that document whether eyeworm infections alter behavior, we feel hunter-donated birds provide a random and unbiased sample. In other words, there is no reason to believe infected and noninfected individuals are harvested at different rates.

We agree with Olsen et al. (2016) in that surveys, as presented here, provide important information, but experimental approaches will ultimately describe the impacts of helminth infections on populations. For example, Robel et al. (2003) examined relationships of helminth burdens, including *O. petrowi,* on demographics of lesser prairie-chickens in Kansas. Prevalence of *O. petrowi* in lesser prairie-chickens was 95% with a mean of 14 and intensities ranging from 1 to 81. Using telemetry data, they compared clutch size, nest success, movement, home range, and April–November survival between parasitized and nonparasitized birds. There were no significant differences among these demographic parameters. Surprisingly, nest success and April–November survival tended to be greater for parasitized than nonparasitized birds, but the differences were not significant. Thus, albeit there is relatively high prevalence and intensity of eyeworms in the Rolling Plains of Texas, we encourage researchers to take more experimental approaches to determine population-level effects.

We conclude that there is an overall absence of eyeworms in bobwhites across most of the bobwhite's range in the United States. However, it is unknown why some areas support high prevalence and intensities of *O. petrowi* in bobwhites. Thus, reintroduction and translocation programs that seek to introduce individuals to naïve areas of low prevalence should consider infection status of individuals as a precaution to avoid unknown impacts. On the other hand, it may also be noted that migratory birds are also known to be infected by *O. petrowi* (Dunham and Kendall 2014). It is likely that environmental conditions that regulate intermediate host occurrence determine geographic prevalence of *O. petrowi* in bobwhites. We contend that the effects of eyeworm infections are a presently unknown, but intriguing, management concern for bobwhite populations in areas of high prevalence and intensities of *O. petrowi*.

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FREE-RANGING, NORTHERN BOBWHITE SUBMISSIONS TO THE SOUTHEASTERN COOPERATIVE WILDLIFE DISEASE STUDY (1982–2015)

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ABSTRACT

There are concerns regarding population declines of northern bobwhite (*Colinus virginianus*) over the past 4 decades (Palmer et al. 2011). Infectious and noninfectious diseases are among the limiting factors that potentially influence bobwhite demographics (Applegate 2014). The last update of diseases of bobwhite was presented at the Second National Quail Symposium in 1982 (Davidson et al. 1982). Since that report, scientists at the Southeastern Cooperative Wildlife Disease Study (SCWDS) have examined 133 wild bobwhites from 13 states. The SCWDS is a cooperative between states and the University of Georgia and obtains cases from the cooperating states. In this update, we focus on the diagnostic testing results from wild birds and exclude other cases that were examined during this period. We searched the SCWDS database for all bobwhite cases 1985–2016 and examined the individual case reports for 133 wild bobwhite quail. During this period, the majority of cases originated from Florida, Georgia, and Kansas, where research was being conducted on bobwhite populations. A diagnosis could not be clearly identified in all cases and some otherwise healthy bobwhites were submitted for screening; therefore, we have narrowed the focus of this report to a subset of 78 bobwhites. Wild bobwhites that were submitted by SCWDS state cooperators had an approximately even distribution between male and female birds (26 F: 19 M; 2 unknown sex). Adults (20 F, 10 M) predominated over juvenile birds (6 F, 7 M, 2 unknown sex). Trauma (physical injury) was the diagnosis in 17 female and 38 male bobwhites submitted during this period. Three each of male and female birds were considered to have no health problems. Some of the most frequent findings in diagnosed bobwhites were possible *Physaloptera* sp. infection ($n = 9$, 17.0%), avian pox ($n = 7$, 14.9%), intoxication (lead and carbamate; $n = 5$, 10.6%), corneal opacity ($n = 4$, 8.5%), *Sarcocystis* sp. infection ($n = 3$, 6.4%), and fungal pneumonia ($n = 2$, 4.25%). Some parasitic infections (e.g., coccidiosis) were thought to be associated with mortality based on necropsy and laboratory findings while a number of the parasites were determined to be incidental findings (e.g., *Sarcocystis* and *Physaloptera*) based on necropsy and laboratory findings. Corneal opacity was found in 4 birds, but the cause was not determined. The most striking findings were that trauma (e.g., physical injury) or avian pox were among the most common causes of mortality in free-ranging quail. Iatrogenic (researcher) causes of mortality ($n = 5$, 10.6%) associated with complications from radiotransmitters and small mammal trapping also occurred. This latter urges careful consideration among bobwhite researchers. The cause of population declines in bobwhites are likely multifactorial. We hope that morbidity and mortality investigations can provide some insight into potential limiting factors for bobwhites and assist wildlife managers with population management decisions.

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Key words: *Colinus virginianus,* diseases, northern bobwhite, parasites, trauma

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A BRIEF HISTORY OF INSECTICIDES AND QUAIL

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ABSTRACT

Humans have employed chemical methods of pest control since the earliest days of agriculture and these substances have affected native wildlife, including quail and other gamebirds (Galliformes), to varying degrees. Several quail species have experienced steep population declines over the past several decades and insecticides may be a contributing factor. Quail are also known to use agricultural habitat for nesting and foraging purposes and are therefore likely to encounter elevated levels of insecticidal chemicals in the soil, vegetation, and insect biomass in that environment. The first commercially available insecticides appeared in the early 1900s with the introduction of arsenic-based compounds (arsenicals). Chemical engineering during World War II resulted in arsenicals being replaced with synthetically produced insecticides such as organochlorine, carbamate, and organophosphate compounds over several decades. Many of these substances have been shown to increase mortality rate, alter behavior, and produce severe reproductive complications in quail, both in the lab and the field. Today, the world's most popular insecticides, neonicotinoids, are being reevaluated for environmental safety following reports that they may be affecting nontarget wildlife. This review examines the types of insecticides that have been used in the United States, how quail could be exposed to these substances, and how they may have contributed to declining quail populations.

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Humans have employed chemical methods of pest control since the earliest days of agriculture and different substances have affected native wildlife, including quail and other gamebirds (Galliformes), to varying degrees. It is well-established that several quail species have experienced a steep population decline over the past several decades. Northern bobwhites (*Colinus virginianus*), for example, have decreased by >80% since the 1960s and insecticide use may be a contributing factor. Quail are also known to use agricultural habitat for nesting and foraging purposes and are therefore likely to encounter insecticidal chemicals in the soil, vegetation, and insect biomass in that environment. Here we examine the types of insecticides that have been used in the United States, how quail could have been exposed to these substances, and how their toxic effects may have contributed to diminishing quail populations.

ARSENIC

Arsenic compounds were among the first substances used to control agricultural pests (Bolt 2013). Significant concentrations of arsenic occur naturally in the environment, usually in conjunction with metals such as cobalt, nickel, iron, lead and copper (Chou and De Rosa 2003). Commercial varieties of arsenic pesticides became available in the mid-1800s and were used in the United States for >100 years (USDHHS 2016). The insecticides proved invaluable in controlling destructive pests such as the coddling moth, Colorado potato beetle, boll weevil, and horn worm (Eisler 1988, Stone and Anderson 2009). Despite their effectiveness, human health concerns caused arsenicals to be gradually phased out of agriculture (USDHHS 2016). Today, inorganic arsenic compounds are no longer manufactured or employed as insecticides in the United States.

At the height of their popularity in the late 1920s and 1930s, nearly 20,000 metric tons of arsenic-based pesticides were being applied annually in the United States (Reed et al. 2006). Quail and other game birds likely came into contact with these chemicals because quail have been known to use agricultural habitat for nesting and foraging purposes (Puckett et al. 1995) where they would have access to arsenic-contaminated insects as a food source and be subjected to dermal or inhalation exposure (Khan et al. 2014). Although it is not unusual to detect arsenic in soil from naturally occurring deposits, concentrations on farmland tend to be considerably

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greater than background levels as a result of repeated pesticide applications (Chou and De Rosa 2003). Arsenicals are also highly mobile via wind, surface water, and groundwater pathways (Irwin et al. 1997), meaning they can be transported beyond farmland areas to surrounding habitat and impact wildlife outside the immediate site of application.

Both field and laboratory studies have attempted to gauge the effects of arsenicals on wildlife. Laboratory toxicity tests have demonstrated that inorganic arsenic exposure is connected with stunted growth, weight loss, lethargy, and neurological abnormalities in chickens (*Gallus gallus*)—birds that are physiologically similar to quail (Khan et al. 2014). However, in an experiment designed to mimic field conditions, northern bobwhite hatchlings were fed grasshoppers killed with arsenic trioxide with no detectable impact (Eisler 1988). Arsenicals have also been shown to be quickly metabolized and excreted by gallinaceous birds; in chickens subjected to a diet laced with sodium arsenite, only 2% of the original dose remained in their systems after 60 hours (Eisler 1988). Another study demonstrated that woodpeckers (*Picoides dorsalis, P. villosus*) that fed on arsenic-laced beetle larvae experienced no debilitating effects despite elevated arsenic levels in their blood (Morrissey et al. 2007). Field evidence, coupled with the fact that no large-scale bird mortality events have been attributed to arsenic poisoning, suggests that arsenic-based pesticides may not have been a significant threat to quail even at the height of their use.

It appears unlikely that arsenicals have been a major contributor to declining quail populations. However, the human health impacts of arsenic-based insecticides (cardiac and respiratory disorders, cancers, etc.) meant that they would eventually be replaced. No effective substitute was found until World War II, when fervent interest in chemical engineering produced new classes of synthetic pesticides.

ORGANOCHLORINES

The advent of organochlorines (OCs) marked a new era for insecticides heralded by dichlorodiphenyltrichloroethane (DDT). Dichlorodiphenyltrichloroethane featured broad-spectrum toxicity to insects with the desired low toxicity to mammals and its half-life in the environment was measured in decades (USDHHS 2000, Hoffman et al. 2003). Its persistence, combined with the fact that it was largely insoluble in water and therefore unlikely to be washed away (Delaplane 1996, Muir 2012), reduced the need for reapplication. The insecticide was such a success that its discoverer, Paul Hermann Müller, earned the Nobel Prize in Physiology or Medicine in 1948 (Strandell 2009).

Although DDT and other organochlorines proved effective in controlling a variety of pests, they also had impacts on nontarget wildlife. Birds and mammals experienced neurotoxic effects in the form of uncontrolled muscle contractions and hyperactivity (Bradbury and Coats 1982, Lal and Saxena 1982). The estrogen-mimicking properties of OCs also interfered with avian reproduction by altering the timing of egg laying and producing abnormally thin eggshells. Birds that tried to incubate thin-shelled eggs crushed them in the attempt, resulting in population crashes in several species (Giguere 2008, Muir 2012). Dichlorodiphenyltrichloroethane's primary metabolite, dichlorodiphenyldichloroethylene (DDE), has a tendency to concentrate at higher trophic levels, meaning predatory birds were most severely affected (Connell 1999, Hoffman et al. 2003).

In determining whether quail were also affected, it is first necessary to consider how they might have been exposed. Dichlorodiphenyltrichloroethane was historically used to protect a variety of food crops including cotton, peanuts, and soybeans (NPIC 2000) and quail have been observed in similar agricultural habitat during periods of pesticide application (Palmer et al. 1998). In addition to crop spraying, organochlorines were applied directly to soil and aquatic environments to target specific pests (Lal and Saxena 1982) and detectable levels have remained many decades after use. These residues are subsequently carried by the movement of wind or water to new environments where organisms may be exposed via ingestion, respiratory, or dermal routes (Lal and Saxena 1982, Hoffman et al. 2003). Despite the tendency for quail to eat low on the food chain, organochlorine pesticides have been detected in scaled (*Callipepla squamata*) and bobwhite quail tissues (Baxter et al. 2015).

The effects of OC exposure on quail are varied. The eggshell thinning that was so well-documented in predatory birds appears to be less of a problem for galliforms because Japanese quail (*Coturnix japonica*) and chickens have shown only minor changes in eggshell thickness following exposure to DDT (Bitman et al. 1969, Peakall and Lincer 1996). However, other work has indicated that embryonic exposure to DDE can alter brain structure and interfere with reproduction by accelerating the onset of puberty in female Japanese quail and reducing sexual behaviors in males (Quinn et al. 2008, Mura et al. 2009). Given that quail rely on high rates of reproduction for maintaining populations (Brennan 2014), these changes could have impacts at the landscape level. Organochlorines have also been shown to enhance the toxicity of other substances. Adult male Japanese quail that were pretreated with dietary DDE were more susceptible to subsequent applications of an organophosphate compound, parathion (Ludke 1977). Similarly, pretreatment with the organochlorine endrin has been shown to increase accumulation of another OC, chlordane, in northern bobwhite brain tissue (Hoffman et al. 2003).

Reproductive impacts and synergistic effects with other toxicants make organochlorines a potential factor in the quail decline. Although DDT was effectively removed from the U.S. market in 1972 (USEPA 2016), its residues and effects lingered for decades after the ban. The elimination of organochlorines also left a void to be filled by new types of insecticides.

ORGANOPHOSPHATES AND CARBAMATES

Organophosphate (OP) and carbamate (CB) pesticides are used as insecticides, herbicides, and fungicides on agricultural lands, rangelands, forests, wetlands, and residential and commercial areas (Smith 1987, Glaser 1999). Most widely used OP and CB insecticides are highly toxic but relatively short-lived in the environment (Smith 1987, Glaser 1999, Hill et al. 2012), making them an acceptable replacement for the highly persistent, bioaccumulative organochlorines (Hassall 1982, Smith 1987, Hill 2003). Both OPs and CBs were introduced into commercial use in the 1950s (Kuhr and Dorough 1976, Smith 1987).

Of the 2 classes, OPs are more ubiquitous and comprise more than one-third of the registered pesticides on the world market (Hill 2003). In the United States alone there are approximately 70 organophosphorus pesticides registered as active ingredients in thousands of products, such as chlorpyrifos and methyl parathion (Hill 2003). The OP Glyphosate was the most used pesticide active ingredient in 2007 with 180–185 million pounds applied (USEPA 2016). In contrast, there are approximately 50 registered carbamate-based pesticides available (Hill 2003). Of the 50, only 8 are used for insect control and 3 of the 8—carbofuran, methomyl, and carbaryl—account for >90% of use (Hill 2003).

Common routes of exposure for birds to OP and CB pesticides include consumption of treated seeds, pesticide-coated vegetation, poisoned insects, direct ingestion of pesticide granules, and contaminated water (Dimmick 1992, Glaser 1999). Inhalation and absorption through the skin are also possible (Glaser 1999). Quail are often found in or near agricultural lands, so they are particularly vulnerable to exposure to OPs and CBs used to treat crops (Dimmick 1992). Bobwhite quail chicks may be more susceptible to exposure via consumption of poisoned insects because they feed almost exclusively on insects during the first few weeks posthatch (NRCS 1999). Similarly, adult bobwhites may be at greater risk of exposure by eating pesticide-coated seeds and vegetation because these constitute the majority of their diet (NRCS 1999, Hernández and Guthery 2012).

Birds seem to be particularly sensitive to the effects of OPs and CBs (Grue et al. 1997, Glaser 1999, Hill 2003), which have been shown to produce physiological, behavioral, and reproductive effects in quail and other avian species. Studies have demonstrated an increase in mortality following ingestion of these pesticides in bobwhites (Brewer et al. 1996) and mallard ducks (*Anas platyrhynchos;* Martin 1990). The organophosphate methyl parathion has been known to alter brain chemistry in bobwhites, with subsequent effects on activity level and coordination along with increased predation rates (Galindo et al. 1985, Buerger et al. 1991). Feeding behavior is known to be affected as well: bobwhite chicks dosed with methyl parathion exhibited decreased food-seeking activity and failed to discriminate between treated and untreated food (Bussiere et al. 1989), though other work suggests that they may be able to detect and avoid pesticide contaminated feed when given sufficient alternatives (Bennett 1989). There is also evidence that organophosphates and carbamates may suppress immune system function (Nain et al. 2011), slow hatchling growth and development (Martin et al. 1991), and reduce egg production and hatching rate (Rattner et al. 1982, Stromborg 1986, Kilbride et al. 1992).

Exposure to OP and CB pesticides could therefore contribute to the decline of quail by increasing mortality (directly or through abnormal behavior that increases predation), altering feeding habits, rendering birds immunocompromised or interfering with reproduction. These chemicals are still used today, alongside a new class of insecticides: the neonicotinoids.

NEONICOTINOIDS

When neonicotinoids first entered the market in the early 1990s, they appeared to address the concerns associated with earlier compounds. This new class of insecticides was effective as a form of pest control but possessed a high degree of selectivity to insects (Jeschke et al. 2013), making them safer for human use than the organochlorines, organophosphates, and carbamates. They are most often applied as a seed coating, which is absorbed into plant tissues, localizing the protectant and reducing contamination to the environment (Goulson 2013, Simon-Delso et al. 2014). In the years that followed their introduction, neonicotinoid compounds became the most widely used insecticides in the world (Gibbons et al. 2014).

As the name implies, neonicotinoids behave similarly to nicotine, a chemical that is produced in some plants as a pest deterrent (Gotti and Clementi 2004, Seifert and Stollberg 2005). The toxic effects of nicotine derive from the fact that it mimics the neurotransmitter acetylcholine, overstimulating the nervous system and causing death in insects (Yamamoto and Casida 1999). Neonicotinoids differ in that they are more strongly attracted to receptors in the invertebrate nervous system than the vertebrate one (Millar and Denholm 2007).

The insecticide's ability to translocate into plant tissues would theoretically keep environmental concentrations low and minimize exposure to quail and other wildlife, but data suggest that field concentrations are higher than anticipated. It is estimated that approximately 5% of the pesticide in a seed coating is absorbed by the plant while the rest blows away during sowing or is deposited in the surrounding soil and water (Goulson 2014). The lubricating powder that facilitates sowing can contain active ingredient concentrations up to 15,000 μg/g (Bonmatin et al. 2015) and is often released to the environment after use. Neonicotinoids are purported to be denatured relatively quickly in direct sunlight; however, half-lives have been shown to exceed 1,000 days in soil and water mediums. Several studies have detected environmental neonicotinoid concentrations that far exceed the amounts needed to control pests (Goulson 2013, Gibbons et al. 2014, Hladik et al. 2014). Some seed is frequently spilled during the sowing process or buried shallowly enough that it can be scratched out (Mineau and Palmer 2013), making the coated seeds themselves a potential source of contact. Plausible routes of exposure for quail therefore include ingestion of coated seeds and environmental residues at greater concentrations than those predicted by normal use.

Despite being engineered for low toxicity to vertebrates, there is evidence of neonicotinoids affecting quail and other birds. There have been reports of avian mortalities in the field attributable to neonicotinoid ingestion as determined by crop and tissue analysis (Berny et al. 1999). Abnormal behaviors, including lethargy, ptiloerection, and impaired locomotor ability, have also been documented in both lab and field investigations following consumption of neonicotinoid coated seeds (Berny et al. 1999, Poppenga and Tawde 2012, Tokumoto et al. 2013). Data suggest that neonicotinoids may decrease clutch size and embryo survival rates in bobwhites (Fernandez-Perea et al. 2009) or produce ovary malformations in laying hens (Hoshi et al. 2014). Neonicotinoids and their metabolites have also been known to exert genotoxic effects, resulting in cancer and DNA fragmentation in germ cells (Casida 2011, Gibbons et al. 2014, Hoshi et al. 2014). By increasing mortality of adult birds through direct toxic effects or increased predation, and by affecting reproductive efforts through decreased egg production, reduced embryo survival, and genetic complications, neonicotinoids become a potential contributor to declining quail populations.

MANAGEMENT AND RESEARCH IMPLICATIONS

The history of insecticide use in the United States makes it clear that they are potential contributors to quail population declines and have important implications for quail management. For many of the compounds described above, the full extent of their impact—field-realistic concentrations, interactions with other potentially toxic substances, effects specific to avian or embryonic physiology—were not understood until after they had been in use for some time. There is, of course, testing that takes place before any pesticide is made commercially available; however, it is difficult to account for all field-realistic variables, every species, and every possible type of effect. The most effective way to minimize the impact of insecticides on quail populations is to limit their use as much as possible by taking advantage of alternative pest control methods. Integrated Pest Management calls for the cultivation of pest-resistant crops; employment of insect pheromones in controlling and monitoring pest species; and the use of predators, pathogens, and parasites to reduce insect damage without insecticides (Abrol 2013). In areas where management goals are more aligned with ranching than crop cultivation, simply maintaining a diverse, native grassland habitat is an effective way to discourage pest species. Nonchemical methods for achieving this include disking, burning, and hoof traffic, which can be used to control for both plant and insect pests (Martin 1983, Hernández and Guthery 2012).

Future research can also help minimize the effects of insecticides on quail populations. Toxicity studies should focus on determining field concentrations based on persistence and real rates of application, which may differ from application instructions. There should also be greater emphasis placed on determining impacts on embryos and chicks, which may be more susceptible to chemical exposure than adult birds. Research that contributes to the improvement of nonpesticide methods of control can also help reduce insecticide use in quail habitat.

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USE OF *EXTINGUISH PLUS*™ TO REDUCE RED IMPORTED FIRE ANTS AND INCREASE NORTHERN BOBWHITE ABUNDANCE

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ABSTRACT

Populations of northern bobwhite (*Colinus virginianus*) have been declining throughout Texas since at least the 1970s. The red imported fire ant (RIFA, *Solenopsis invicta*) was introduced from South America and reached Texas by the 1950s. Previous studies have documented the negative effects of RIFA on northern bobwhite populations through both direct predation and indirect reduction of small invertebrates. In 2013, 2014, and 2015, large areas (1,490 ha in 2013 and 2,380 ha in 2014 and 2015) of the 3,744-ha portion of the Attwater Prairie Chicken National Wildlife Refuge (APCNWR) in Colorado County, Texas, were aerially treated with *Extinguish Plus*™, a chemical pesticide and reproductive inhibitor that targets ants. Our study took place on APCNWR and our objectives included evaluation of the impacts of RIFA treatment on 1) RIFA abundance, and 2) northern bobwhite nest success and brood survival. We trapped, banded, and radiocollared northern bobwhites in areas treated and not treated with *Extinguish Plus* from May 2014 through August 2016. We also collected RIFA abundance data using baited Petri dishes on areas treated and nontreated areas during these periods. Treatment reduced RIFA presence on the refuge by 73.4% during 2014 and 2015, but did not reduce RIFA presence during 2016 possibly because of displacement of RIFA colonies due to heavy flooding on the refuge. We detected a difference ($\chi^2_1 = 11{,}009$, $P = 0.0009$) in the number of females sighted with and without broods between treated (19.5% F with broods) and nontreated areas (35.7% F with broods). We also found a difference ($t_{12} = 2.51$, $P = 0.027$) in mean number of chicks per brood sighted within treated (4.7) versus nontreated (9.3) areas for 2014 and 2014; but in 2016, we found no difference ($t_{12} = 0.32$, $P = 0.754$) in mean number of chicks per brood sighted within treated (7.7) and nontreated (8.4) areas, which was possibly due to extensive flooding in the nontreated area in April that destroyed most first nests. Our data suggested treatment with *Extinguish Plus* did not increase northern bobwhite abundance on the APCNWR during the 2014, 2015, and 2016 bobwhite nesting seasons. Our results differ from previous studies, possibly because of time since treatment and differences in environmental factors between treated and nontreated areas such as ecological site, vegetation composition, and predator abundance.

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Key words: brood survival, *Colinus virginianus,* northern bobwhite, red imported fire ant, *Solenopsis invicta*

Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) numbers have been on the decline throughout Texas since at least the 1970s (Bridges et al. 2001). Red imported fire ants (RIFA; *Solenopsis invicta*) were introduced to the United States from South America at

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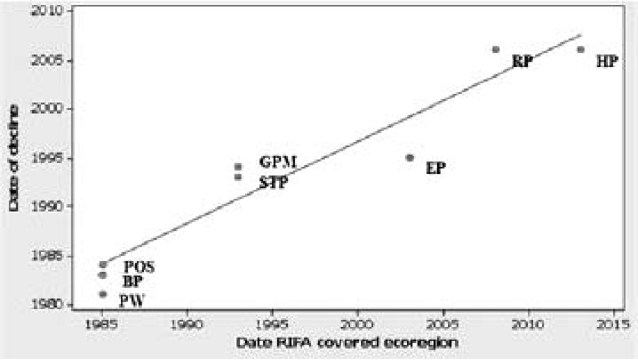

Fig. 1. Correlation of spread of red imported fire ants across ecoregions by date with northern bobwhite declines across ecoregions (PW = Pinywoods, BP = Blackland Prairies, POS = Postoak Savannas, STP = South Texas Plains, GPM = Gulf Coast Prairies and Marshes, EP= Edwards Plateau, RP = Rolling Plains, and HP = High Plains) of Texas, USA (from Caldwell 2015).

Mobile, Alabama, around the 1920s (Drees and Vinson 1993). Red imported fire ants began a steady spread through the southern United States, reached Texas in the 1950s, and spanned the state by 2013 (Caldwell 2015). Caldwell (2015) found a direct correlation between the spread of RIFA and the decline of bobwhite in Texas (Fig. 1).

A number of studies have reported that RIFA will prey on young birds, including bobwhites (Drees 1994, Allen et al. 1995, Mueller et al. 1999, Campomizzi et al. 2009). Red imported fire ants are known to kill both hatchling bobwhite chicks and older chicks (Mueller et al. 1999). In experimental trials, captive-reared bobwhites spent time and effort responding to RIFA exposure, which decreased time and effort devoted to other activities, thereby reducing fitness (Pedersen et al. 1996). According to Giuliano et al. (1996) bobwhite chicks experienced reduced survival when exposed to as few as 50 RIFA for 60 seconds compared with chicks not exposed to RIFA. Red imported fire ants are known to negatively impact bobwhites by preying on invertebrates, which are a major food source for bobwhites (Savory 1989, Wojcik et al. 2001). Porter and Savignano (1990) found that arthropods were reduced by 75% following RIFA invasion. If a lack of small insects and other invertebrates exists to feed young bobwhite chicks, malnutrition, dehydration, and death may follow hatching. Morrow et al. (2015) documented the importance of invertebrate abundance to the Attwater's prairie-chicken (*Tympanuchus cupido attwateri;* APC). They concluded that strong invertebrate populations were essential to APC brood survival, and to the long-term recovery of this critically endangered species. They also documented that RIFA had a clear negative impact on invertebrates during their study.

The decline of bobwhites has been concurrent with the westward spread of RIFA (Allen et al. 1995). This correlation may represent a long-term negative impact through direct predation or indirectly through insect reduction. Chemical reduction of RIFA may contribute to the recovery of bobwhite populations (Allen et al. 1995, Mueller et al. 1999).

Our research hypotheses were the following: 1) treatment of areas with *Extinguish Plus*™ would reduce the abundance of RIFA; 2) bobwhite nest success would be greater in areas treated with *Extinguish Plus*; and 3) bobwhite brood survival would be greater in areas treated with *Extinguish Plus*. If significantly more bobwhite chicks survived to fledgling age and more fledglings survived to adulthood in the treated areas of the refuge than in the nontreated areas, it could be inferred that chemical reduction of RIFA was successful at increasing bobwhite nest success and brood survival.

STUDY AREA

We conducted research on the 3,744-ha portion of the Attwater Prairie Chicken National Wildlife Refuge (APCNWR) located approximately 97 km west of Houston, Texas, in Colorado County. The APCNWR was dedicated to management of the critically endangered APC. The refuge was located on the border between the Gulf Prairies and Marshes and the Post Oak Savannah ecoregions. The refuge was bordered primarily by agricultural fields and properties infested with woody vegetation. Common ecological sites on the refuge included loamy prairie, coarse sand, and claypan prairie (Fig. 2). Little bluestem (*Schizachyrium scoparium*) was the dominant grass in the climax community of the APCNWR, accompanied by a wide diversity of primarily native grasses and forbs. Grasslands were managed for a heterogeneous landscape by burning 16–28-ha patches on a 4-year rotation (Fuhlendorf and Engel 2001, Fuhlendorf et al. 2006). Light to moderate grazing was used at the refuge. Herbicide treatment of individual plants and limited spot-treatment of brush and nonnative plant species occurred on the refuge.

Control of potential APC nest predators also was done on APCNWR. During 2014, 32 feral hogs (*Sus scrofa*), 4 Virginia opossum (*Didelphis virginiana*), 7 raccoons (*Procyon lotor*), and 21 striped skunks (*Mephitis mephitis*) were removed by Wildlife Services from the refuge; and during 2015, 5 feral hogs, 7 Virginia opossum, 5 raccoons, and 18 striped skunks were removed. During 2016, 122 feral hogs, 8 Virginia opossum, 11 raccoons, and 28 striped skunks were removed. Bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) were not controlled on the refuge; however, they are known to prey on northern bobwhite nests (Staller et al. 2005).

In Columbus, Texas (16 km W of the refuge), rainfall totaled 105.2 cm in 2014 (Fig. 3), of which 33.6 cm fell in May (National Centers for Environmental Information; www.ncdc.noaa.gov). The highest rainfall recorded in a 24-hour period during May 2014 was 21.1 cm (National Centers for Environmental Information; www.ncdc.noaa.gov). During January–June 2015, 107.3 cm of rainfall was recorded (Fig. 4). The highest rainfall recorded in a 24-hour period (28 cm) during 2015 occurred when Tropical Storm Bill hit the Texas Gulf Coast on 16 June 2015. A

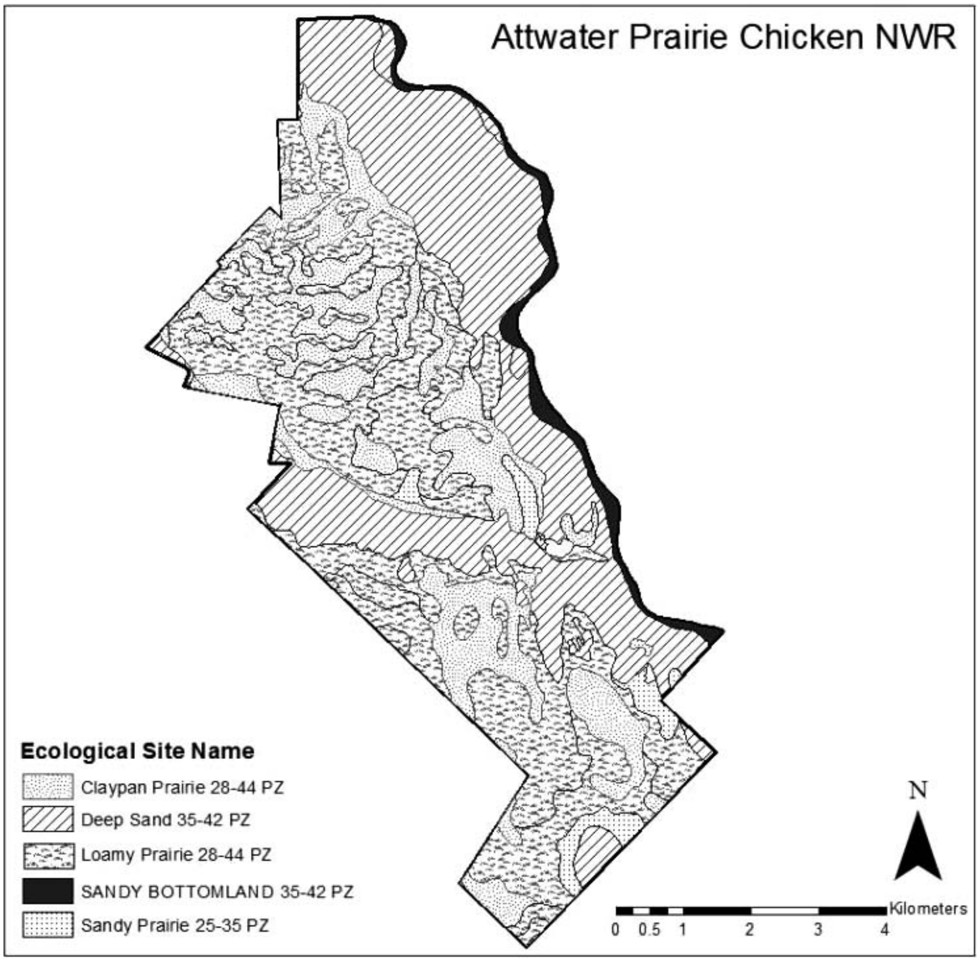

Fig. 2. Ecological sites, Attwater Prairie Chicken National Wildlife Refuge, Colorado County, Texas, USA (http://sdmdataaccess.nrcs.usda.gov/).

typical year's amount of rainfall had occurred by the end of June 2015 and below-average rain then was received in August 2015 (Fig. 4). From January to August 2016, 109.4 cm of rain was received at the refuge (U.S. Climate Data; www.usclimatedata.com). The greatest rainfall recorded in a 24-hour period (24 cm) during 2016 occurred on 18 April; however, upstream from Coushatta Creek (which ran through the refuge) and the San Bernard River (the east boundary of the Colorado County portion of the refuge) up to 41 cm of rainfall was recorded on 18 April 2016, which caused major flooding of the refuge (Fig. 5).

In October 2013, in September–October 2014, and again in October 2015, portions of the APCNWR were aerially treated with *Extinguish Plus* (Wellmark International, Schaumburg, IL, USA; Fig. 6), a chemical pesticide and reproductive inhibitor that targets ants. *Extinguish Plus*™, approved for rangelands in 2007, contains both an adulticide (Hydramethylnon) and an insect growth regulator (S-Methoprene), which allows for the sterilization of queens and the killing of worker ants (Extinguishfireants.com; http://www.extinguishfireants.com/products.php?type=nursery). According to the manufacturer's website, *Extinguish Plus* is known to be toxic only to ants and fish. The bait is taken up quickly (within <2 hr) by ants (Calixto et al. 2007), is slow to act, and requires 3–6 months to take full effect when applied in the autumn (Calixto et al. 2007, Nester 2013). Although all ants are susceptible to this product, fire ants dominate bait products such as *Extinguish Plus* because of their aggressive foraging behavior (Calixto et al. 2007). According to Nester (2013), full effect of the product varies with reinvasion pressure; however, 1 application/year is usually sufficient. *Extinguish Plus* was applied at 1.7 kg/ha (1.5 lbs/ac) to 1,490 ha (40% of area in 2013) and 2,380 ha (64% of area in 2014 and 2015) of the 3,744 ha-portion of the refuge in Colorado County. Although the treatment was applied by the U.S. Fish and Wildlife Service to promote APC recruitment, it allowed us an opportunity to determine the effects of large-scale chemical treatment of fire ants on bobwhite abundance, nest success, and brood survival as well as food invertebrate abundance. The effects of such large-scale treatment of RIFA on bobwhites and their food invertebrates have not been studied extensively. The purpose of our research was to determine whether large-scale RIFA treatment is an effective method of increasing bobwhite abundance.

We conducted research on treated and nontreated areas of APCNWR. Locations for treatment were selected

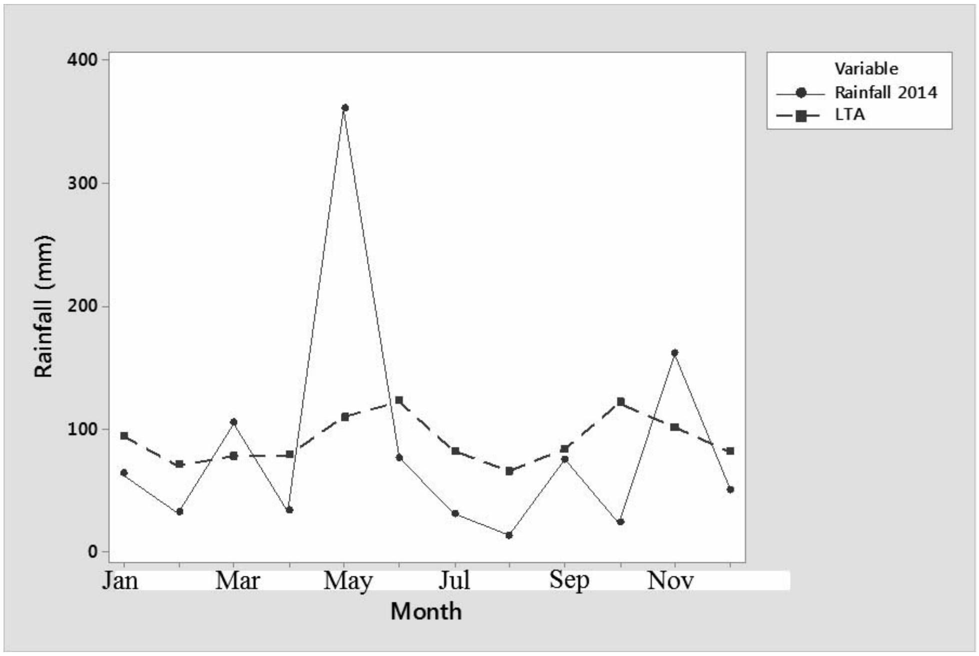

Fig. 3. Rainfall by month in 2014 and 30-year average (LTA) at Columbus, Texas, 16 km west of Attwater Prairie Chicken National Wildlife Refuge in Colorado County, Texas, USA.

by U.S. Fish and Wildlife Service personnel to maximize benefit to APC. This resulted in a number of environmental differences or biases between treated and nontreated areas of the refuge including ecological sites, vegetation composition, rainfall, and predator abundance. For example, in 2014 treated areas consisted largely of claypan prairie and loamy prairie ecological sites, while 4 pastures in the nontreated areas contained large amounts of coarse sand and corresponding vegetation. However, in 2015, 2 of the coarse sand areas were treated for RIFA leaving only 2 others in the nontreated. In addition, 3 pastures in the nontreated area and 1 pasture in the treated area had been leveled and were former rice fields under restoration to prairie plant communities. These leveled pastures were more likely to retain water from rainfall longer and were in generally lower successional states than other nonleveled pastures. Differences such as these resulted in a level of bias that may have influenced RIFA

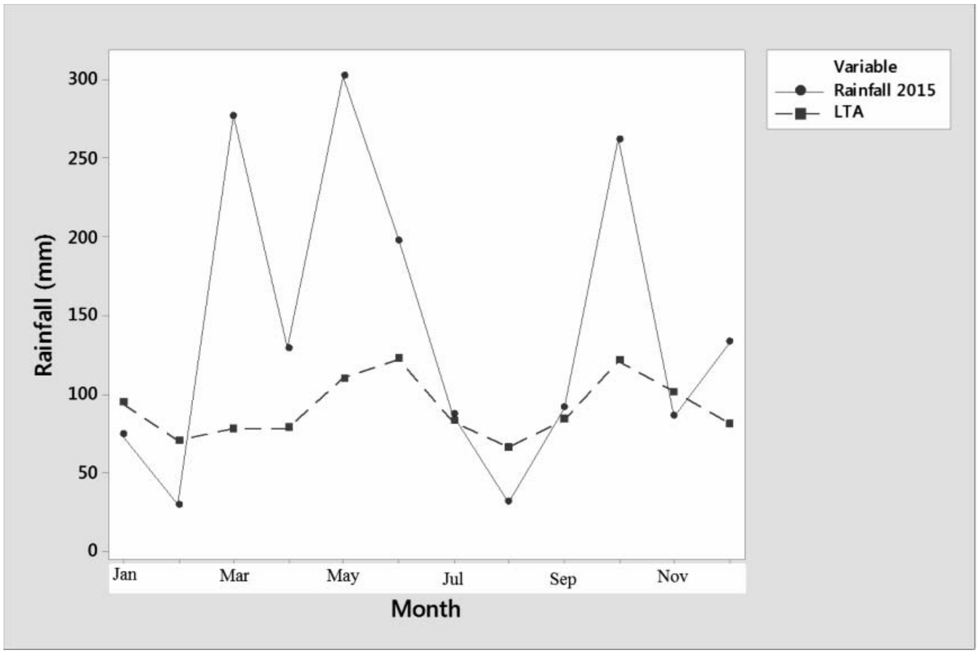

Fig. 4. Rainfall from by month in 2015 and 30-year average (LTA) at Columbus, Texas, 16 km west of Attwater Prairie Chicken National Wildlife Refuge in Colorado County, Texas, USA.

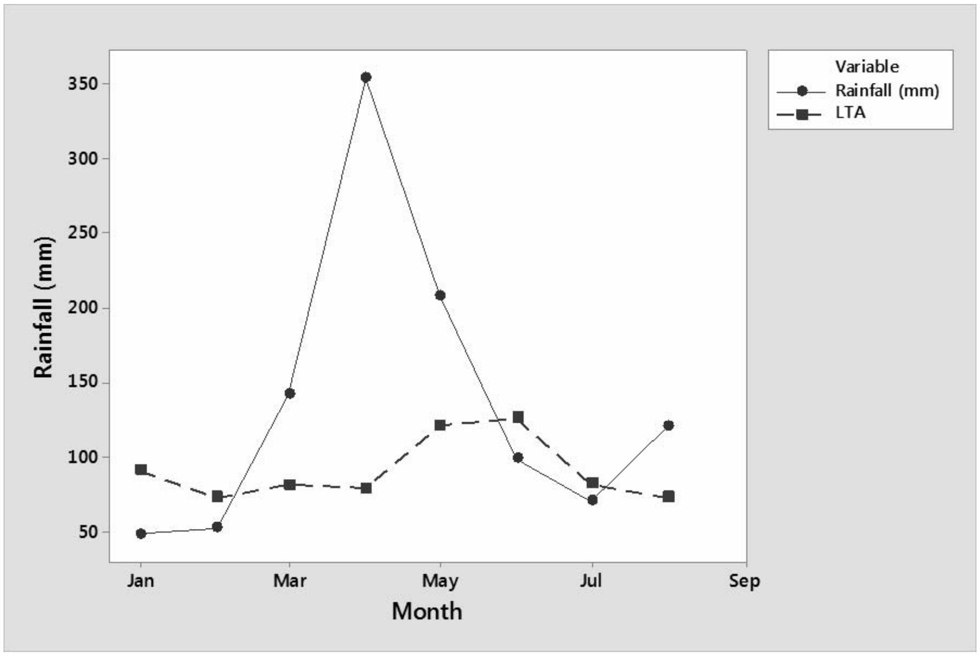

Fig. 5. Rainfall from by month in 2016 and 30 year average (LTA) at Columbus, Texas, 16 km west of Attwater Prairie Chicken National Wildlife Refuge in Colorado County, Texas, USA.

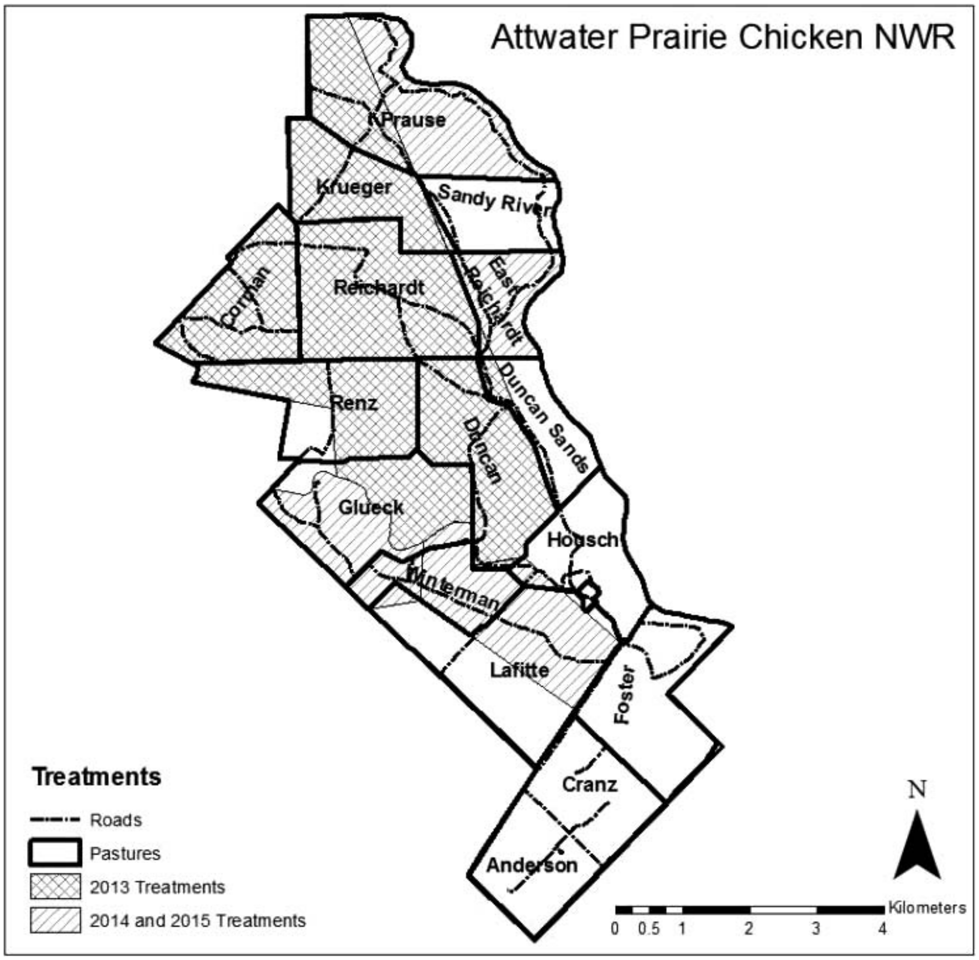

Fig. 6. Areas of Attwater Prairie Chicken National Wildlife Refuge (Colorado County, TX, USA) treated with *Extinguish Plus*™ in 2013, 2014, and 2015 to control for red imported fire ants (map provided by Refuge personnel).

or bobwhite abundance in treated and nontreated areas of APCNWR during our study.

METHODS

Fire Ant Abundance

We estimated relative abundance of red imported fire ants once monthly during May–August 2014 and April–August 2015 and 2016 during the bobwhite nesting seasons at 26 locations randomized each month across the treated and nontreated areas of the refuge. We placed 2 Petri dishes baited with hot dog slices (commonly used for RIFA sampling; Morrow et al. 2015) within 3 m at each site and left them exposed to surrounding ants for 20 minutes. We collected dishes, sealed them with tape to capture any ants inside, and then froze them. We later keyed ants to species (Cook et al. 2014) and counted individuals of each species. We compared total numbers of RIFA collected for both the treated and nontreated areas of the refuge to determine an estimated percent reduction of RIFA following treatment. We used Chi-square tests to determine whether there were differences in the number of ant samples with RIFA between treated and nontreated areas (Ott and Longnecker 2008).

Trapping and Marking

Beginning in April 2014, the start of the bobwhite nesting season and 6 months after treatment with *Extinguish Plus*, we trapped bobwhites according to Texas A&M University Animal Use Permit (AUP) Institutional Animal Care and Use protocol 2014-0012 using funnel traps (Kuvlesky et al. 1989). We selected trap locations based on the following criteria: near heavy escape cover, visible to the investigators from a vehicle on refuge roads, relatively hidden from public view, and near epicenters of audible bobwhite mating calls or bobwhite sightings.

We prebaited potential trap locations weekly with commercially purchased grain mixes that included cracked corn, milo, sunflower, millet, and wheat seeds. Prebaiting continued until final trap locations were selected based on grain disappearance week-to-week. In 2014, we placed bait stations along13.0 km of roads in both treated and nontreated areas. However, in 2015 and 2016, we placed bait stations along 15.1 km of roads in the treated area and along 10.2 km of roads in the nontreated area.

Once we chose promising locations and following ≥ 1 week of prebaiting, we began trapping. Twice-weekly trips to the refuge consisted of baiting all chosen sites, placing a funnel trap at each site, and checking all sites hourly for trapped bobwhites. We aged bobwhites by primary covert color, sexed each by head color (Lyons et al. 2012), weighed each, banded each with a size-7, blue colored band (National Band and Tag Company, Newport, KY, USA) on the right leg, and fitted each with an 8.0-g ($\sim$4% body wt) neckless-style radiotransmitter (150 MHz; Wildlife Materials, Carbondale, IL, USA). We fitted approximately half of the available radiotransmitters on females in the treated area, and approximately half on females in the nontreated area.

Bobwhite Relative Abundance

We used mark–recapture methods to calculate estimates of adult bobwhite relative abundance near our traps in 2014, 2016, and 2016 (Pierce et al. 2012). We used a modified Schnabel method using only known (recaptured or observed after each estimate) adult birds alive at the time of each estimate as the total number marked to obtain conservative relative abundance estimates of bobwhite using our trap sites during June of each year (Silvy et al. 1977).

Nest Success and Brood Survival

Initially, we were going to determine nest success. However, during 2014, we made no attempts to locate active nests because Mueller et al. (1999) observed high abandonment rates (7% [6 of 79] in 1997 and 15% [13 of 87] in 1998) while attempting to locate active nests. Additionally, we had fitted only 5 females with radiotransmitters by 1 June 2014, which provided a very small sample size of potentially nesting females. However, in 2015 we made attempts to locate all female bobwhites with radiotransmitters (by triangulation) twice weekly. We located females suspected of nesting by using a handheld 3-element yagi antenna (Wildlife Materials). We did not attempt to flush a setting female off her nest, but if a female did flush, we noted the number of eggs within the nest. We determined a Global Positioning System location for each nest so we could locate it later. We checked females on confirmed nests (by triangulation) 3–4 times/week during midday (assuming the female would not be off-nest feeding during the heat of the day) for signs they had left their nests. If the female was off the nest, we checked to determine whether the nest had hatched or been lost to predation.

To estimate brood survival in treated and nontreated areas without influencing brood survival by flushing radiotagged female s with broods during 2014, we recorded all females sighted or trapped with and without broods in treated and nontreated areas and recorded the number of chicks per brood. We collected these data once we sighted the first brood on 10 June 2014 and continued until 31 August 2014. During 2015 and 2016, we first observed broods in June and again collected data until 31 August of each year. We sighted broods while driving refuge roads while collecting data for other aspects of this study, but we made most sightings while trapping (trapping conducted a min. of 2 days/week from Mar through Aug each year). To avoid pseudoreplication, we only used the first observation of a female with a brood for each of the 16 pastures (Fig. 6) of APCNWR because radiotagged females with broods had small (11.5 ha, SD = 5.24 ha) monthly ranges and we never observed them to move between pastures. However, different broods within a given pasture could be determined by location, chick size, or date of sighting thereby providing data on different brood sightings within a given pasture over

Table 1. Total ants and total red imported fire ants (RIFA; sample size in parentheses) collected in each month's sampling by treatment versus nontreatment on Attwater Prairie Chicken National Wildlife Refuge, Colorado County, Texas, USA, 2014–2016.

Month and year	Treated total (*n*)	Nontreated total (*n*)	Treated RIFA (*n*)	Nontreated RIFA (*n*)
May 2014	130 (26)	1,924 (26)	1 (26)	1,054 (26)
Jun 2014	320 (42)	2,441 (36)	134 (42)	2,318 (36)
Jul 2014	1,257 (33)	2,613 (25)	906 (33)	2,379 (25)
Aug 2014	2,418 (24)	1,085 (28)	274 (24)	208 (28)
Apr 2015	292 (26)	998 (26)	5 (26)	768 (26)
May 2015	211 (32)	410 (20)	103 (32)	58 (20)
Jun 2015	826 (34)	322 (18)	313 (34)	64 (18)
Jul 2015	128 (26)	569 (26)	95 (26)	231 (26)
Aug 2015	1,157 (26)	446 (26)	104 (26)	182 (26)
Total 2014–2015	6,739 (269)	10,808 (231)	1,935 (269)	7,262 (231)
Apr 2016	454 (26)	530 (26)	299 (26)	158 (26)
May 2016	138 (26)	766 (26)	64 (26)	286 (26)
Jun 2016	517 (26)	157 (26)	280 (26)	65 (26)
Jul 2016	246 (26)	166 (26)	169 (26)	12 (26)
Aug 2016	3,971 (26)	1,254 (26)	2,256 (26)	1,151 (26)
Total 2016	5,326 (130)	2,873 (130)	3,068 (130)	1,672 (130)
Grand total	12,065 (399)	13,681 (361)	5,003 (399)	8,934 (361)

time. For example, if we sighted a female with bumble bee–size chicks (1–3 days after hatch) in a given area and the next day we sighted a female with flying-size chicks (>7 days after hatch) in the same area, we counted this as 2 females with broods in the area.

To determine the number of females without broods, we used our relative abundance estimates of females in treated and nontreated areas as total females available for these areas. To obtain an estimate of females without broods, we subtracted the number of females with broods from the total number of females available from our relative abundance estimates. We used a Chi-square goodness-of-fit test to determine differences in number of females with and without broods located in treated and nontreated areas. We used a 2-sample *t*-test to determine differences in the mean number of chicks per brood between treated and nontreated areas.

RESULTS

Fire Ant Abundance

Across the project's first season (May–Aug 2014), 1,315 RIFA were found in 17 (13.6%) of 125 samples from areas treated with *Extinguish Plus* and 5,959 RIFA were found in 37 (32.2%) of 115 samples from areas not treated (Table 1). During the project's second season (Apr–Aug 2015), 620 RIFA were found in 20 (13.9%) of 144 samples in treated areas and 1,303 RIFA were found in 31 (26.7%) of 116 samples in nontreated areas. During April–August 2016, 3,068 RIFA were found in 36 (27.7%) of 130 samples in treated areas and 1,672 RIFA were found in 42 (32.3%) of 130 samples in nontreated areas (Table 1). Overall, 5,003 RIFA were collected in 73 (18.3%) of 399 samples from treated areas and 8,934 RIFA were collected in 110 (30.5%) of 361 samples from nontreated areas (Table 1). Lower numbers of samples with RIFA were found in treated areas in 2014 ($\chi^2_1 = 11.850$, $P < 0.001$), 2015 ($\chi^2_1 = 6.713$, $P < 0.01$), and overall ($\chi^2_1 = 15{,}368$, $P < 0.00009$), but not for 2016 ($\chi^2_1 = 0.6593$, $P = 0.6593$). Other ant species collected at bait sites included crazy ants (*Nylanderia terricola*), leaf cutter ants (*Atta* or *Acromyrmex* spp.), pyramid ants (*Dorymyrmex pyramicus*), and harvester ants (*Pogonomyrmex* spp.).

Trapping and Marking

In 2014, 11 traps were established in the nontreated area and 16 traps in the treated area; and in 2015 and 2016, 12 traps were established in nontreated area and 20 traps were established in treated areas. Because 4 trap sites that were in nontreated areas in 2014 were treated in 2015 and 2016, they subsequently became treated trap sites. In 2015 and 2016, 5 additional trapping sites were added to the nontreated areas to increase the sample size in the nontreated areas. From March 2014 through August 2016, 433 bobwhites (205 M, 136 F, and 92 chicks too young to be sexed) were trapped, banded, and released at trap site. Over the course of the project, 437 recaptures took place. During this time, 124 bobwhites were recaptured up to 3 times and 84 were recaptured ≥4 times. One bobwhite male was recaptured 8 times.

During 2014, 68 bobwhites (41 M and 27 F) were radiotagged. Of the 27 radiotagged females, 14 were in the treated area and 13 in the nontreated areas; however, only 5 females were radiotagged before 1 June 2014. In 2015, 43 bobwhites (all F) were radiotagged (28 in the treated area and 15 in nontreated area); and in 2016, 31 females (21 in the treated area and 10 in the nontreated area) were radiotagged.

Bobwhite Relative Abundance

June 2014 had an estimated bobwhite relative abundance of 83 (95% CI = 71–95) bobwhites (54 treated and 29 nontreated), June 2015 had an estimated relative abundance of 82 (95% CI = 64–100) bobwhites (49 treated and 33 nontreated), and June 2016 had an estimated relative abundance of 87 (95% CI = 47–108) bobwhites (60 treated and 27 nontreated) in the areas influenced by our traps. No banded or radiotagged bobwhites captured in the treated areas were recaptured in or observed to move into a nontreated area. The same held for birds captured in nontreated areas.

Nests Success and Brood Survival

Only 1 nest was found (incidentally) during 2014 and all eggs were predated shortly after the nest's discovery in a treated area. During 2015, 17 nests were located and only 1 nest hatched (in a nontreated area), 3 nests were destroyed as a result of flooding (nontreated area), and 13 were predated (7 in treated area and 6 in nontreated area). During 2016, 12 nests (9 in treated area and 3 in nontreated area) were located. Only 1 (33%) nest hatched (2 females were killed on the nest) in the nontreated area and 6 (67%) nests hatched in the treated area. In 2016, 2 females in the treated area nested twice (1 female lost her first nest and was successful with the second nest, but she was then killed shortly after leaving her second nest; the second female was successful with both nests, but was killed shortly after leaving her second nest).

Pooled data from 2014, 2015, and 2016 demonstrated a difference ($\chi^2_1 = 11{,}009$, $P = 0.0009$) in the number of females sighted with broods versus without broods between nontreated ($n = 56$ females, $n = 20$ females with broods) and treated areas ($n = 77$ females, $n = 15$ females with broods). During 2014 and 2015, the treated area yielded a mean of 6.1 chicks/brood sighted compared with 8.9 chicks/brood in nontreated areas. Nontreated areas had a larger ($t_{12} = 2.51$, $P = 0.027$) mean brood size, which is a trend opposite that which we had hypothesized. However in 2016, the mean brood size for treated (7.7) and nontreated (8.4) areas was nonsignificant ($t_{12} = 0.32$, $P = 0.754$). These data suggest more quail chicks were produced per adult female in nontreated areas. Further support of this was the fact that more ($n = 28$) hatch-year chicks were trapped in 11 traps in the nontreated site traps than hatch-year chicks ($n = 23$) were trapped in the 16 treated site traps in 2014. Trapping was discontinued on 31 July 2015 prior to any hatch-year chicks being captured because the initial 2 years of funding had ended and a final report was due on 31 August 2015. In 2015, 1 radiotagged female in the non-treated area produced a brood with 10 chicks. This female still had chicks when the study ended on 31 August 2015. However, trapping results (Jun–Aug) in 2016 also indicated there were more hatch-year chicks produced in the nontreated area (34 chicks trapped in 15 traps) than in the treated area (19 chicks trapped in 16 traps).

DISCUSSION

Fire Ant Abundance

In 2014 and 2015, with a few exceptions, monthly samples within the nontreated areas contained more RIFA than treated areas during both collection seasons. These data suggest that treatment with *Extinguish Plus* was successful in reducing RIFA on treated areas during the 2014 and 2015 bobwhite nesting seasons. This result is consistent with that of a similar study on the APCNWR by Morrow et al. (2015), which concluded that treatment significantly reduced RIFA. Our result also is consistent with that of Aubuchon et al. (2006), who found decreased abundance of RIFA on 2 different 8-ha grazed pastures in Alabama that had been treated with *Extinguish Plus*—an earlier form of *Extinguish Plus* containing methoprene, but not hydramethylnon. Mitchell and Knutson (2004), as well, found RIFA presence in 2 peanut fields reduced by 85–98% after treatment with *Extinguish*.

However in 2016, except for the May collection, we found more RIFA in the treated area than the nontreated area. This was probably the result of creek and river flooding during 17–18 April 2016 when much of the nontreated area was flooded, which caused RIFA colonies to raft and float out of the area. In addition, river flooding along the eastern boundary of the treated area probably brought RIFA colonies into the treated area from areas north of the refuge. If a colony is flooded during a rainstorm or other high-water situation, the ants cling together and form a living raft that floats on the flood waters (Adams et al. 2011). Once the raft hits dry ground or a tree, rock, or other dry object, the ants can leave the water (Adams et al. 2011).

Bobwhite Relative Abundance

Schnabel estimates of adult bobwhite relative abundance provided an approximate number of individuals within the vicinity of our bait sites. Adult bobwhite estimates were larger in treated sites (66% of total in Jun 2014, 60% in Jun 2015, and 70% in Jun 2016) than nontreated sites. However, the area influenced by our traps was less in the nontreated site because fewer traps were used in nontreated area than treated areas during all 3 years of our study.

Another estimate of bobwhite relative abundance is catch per trap site. The mean number of adult bobwhites captured per trap site was greater in nontreated (2014 = 7.5, 2015 = 4.5, and 2016 = 10.5) than treated (2014 = 5.6, 2015 = 2.9, and 2016 = 8.3) areas during both years, suggesting that bobwhite relative abundance was greater in nontreated areas during both years. The fewer number of quail captured per trap site in 2015 was because data were collected from March to July, whereas in 2014 and 2016 data were collected from March to August. Allen et al. (1995) found, where bobwhite densities (call counts) were monitored for 2 years after treatment on 5 treated and 5 nontreated areas, that only in the second year after treatment were autumn bobwhite densities greater ($P = 0.028$) on treated areas.

Nest Success and Brood Survival

Data on bobwhite nest success (only 8 successful nests in 3 yr) were limited to the point that we could not determine whether treatment influenced nest success.

However, Mueller et al. (1999) found no difference in bobwhite nest success between areas treated for RIFA with *Amdro*™ (AMBRANDS, Atlanta, GA, USA) and areas not treated.

Extreme rainfall in May 2014 (Fig. 3), 2015 (Fig. 4), and 2016 (Fig. 5), which led to major flooding on the refuge, probably destroyed most first nests attempted by female bobwhites. Flooding was extensive in 2015 because heavy rainfall occurred from April to June. On 16 June 2015, Tropical Storm Bill dumped >28 cm of rainfall on APCNR. Several bobwhite and APC nests were flooded and 2 female bobwhites and some APC females died due to the flooding. After the June flooding event, second bobwhite nesting attempts were usually placed on small sandy mounds surrounded by water, which led to smaller search areas for predators. This in turn led to high rates of nest depredation. In 2015, only 1 of our radiotagged bobwhite nests hatched and it was placed on the edge of a raised gravel road in the nontreated area of the refuge.

The heavy rains during the nesting seasons of 2014, 2015, and 2016 likely flooded (Fig. 7) many first nesting attempts by bobwhites; however, of nests we observed, the 3 flooded nests in 2015 were in the nontreated area. In 2014, much of the nontreated areas consisted of a coarse-sand ecological site and much of the treated areas consisted of claypan prairie and loamy prairie. However, this was not the case in 2015 and 2016 when the treated area was expanded to include more of the coarse-sand ecological sites of the refuge. It is possible that during May 2014, sandy soils in the nontreated site allowed for better drainage of rainfall and, thus, better first-nest survival, which typically results in larger broods than subsequent nesting attempts (N. Silvy, Texas A&M University, unpublished data). The differential flooding of the nontreated site in 2016 probably eliminated all first nests in the nontreated area; however, this was not the case in the treated site where we found 2 nests with 18 and 17, respectively (date and clutch size indicating first nests). Both nests located in the nontreated site contained 11 and 9 eggs, respectively, indicating a second nesting attempt. Heavy rainfall during the flood in April 2016 also affected first nests in the treated area as most nests located in the treated area contained 7–13 eggs, indicating they were second or third nesting attempts. Also in 2016, we observed 1 female that died in the treated area due to flooding of a low area by the heavy rainfall. In addition, we saw fewer females with broods in treated areas.

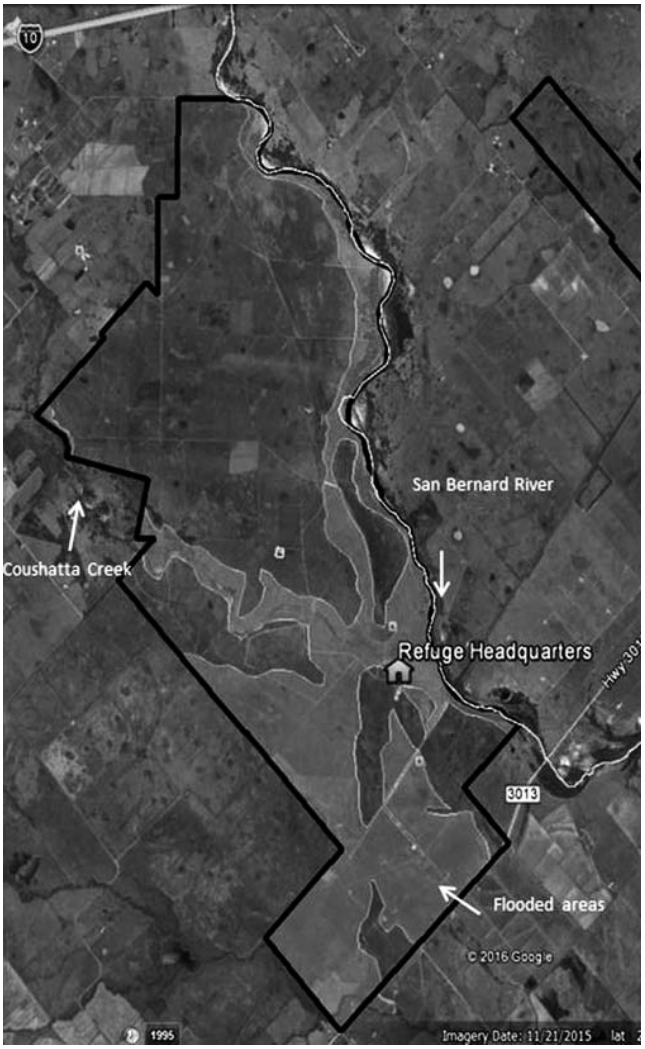

Fig. 7. Areas of Attwater Prairie Chicken National Wildlife Refuge, Colorado County, Texas, USA, flooded by heavy rains on 18 April 2016. (Map generated by J. Magera, Deputy Refuge Manager, Attwater Prairie Chicken National Wildlife Refuge, based on his personal observations of the flooding).

During our study, we found more bobwhite chicks survived to fledgling age per female in the nontreated area of the refuge. These results are not consistent with those of Mueller et al. (1999), who observed bobwhite brood survival to 3 weeks was greater for broods that hatched in treated areas. Morrow et al. (2015) concluded that strong invertebrate populations were essential to APC brood survival, and to the long-term recovery of this critically endangered species. Also, Morrow et al. (2015) observed that APC broods on APCNWR located in areas with the greatest median invertebrate count (338 invertebrates/25 sweeps) had a survival probability of 0.83 at 2 weeks posthatch compared with 0.07 for broods located in areas with the smallest median invertebrate count (18 invertebrates/25 sweeps). Allen et al. (2001) also noted that loggerhead shrike (*Lanius ludovicianus*) and native insect abundance were reduced in areas associated with RIFA. It is possible that our results are related to factors other than those that we researched, such as predator abundance, vegetation succession, or rainfall differences between the treated and nontreated areas of the APCNWR in 2014, 2015, and 2016. Grasslands in the treated area were managed for APCs in a higher successional state with less woody cover than may have been optimal for bobwhites (USFWS 2010). Extreme amounts of rainfall received during all 3 years of our study (Figs. 3, 4, and 5) not only affected bobwhites directly, but also likely adversely affected invertebrates as well, irrespective of RIFA treatment (Uvarov 1977). Given that availability of insects is an important driver of bobwhite chick survival (Savory 1989, Wojcik et al. 2001), these extreme precipitation patterns may have negated any potential benefits to insect abundance resulting from RIFA suppression. It also is possible that ecological site and associated vegetation composition differences between treated and nontreated areas influenced our results.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The bobwhite is an ecologically and economically important game bird species that is experiencing a decline. Although large-scale treatment of ants with *Extinguish Plus* on the APCNWR was initiated as a management action for the critically endangered APC, it also provided us an opportunity to evaluate the effectiveness of large-scale RIFA reduction on bobwhite abundance.

Based on our study, we drew the following conclusions:

1. Treatment with *Extinguish Plus* reduced RIFA relative abundance in 2014 and 2015, but not in 2016.
2. Because of small sample size, we could not conclude whether treatment with *Extinguish Plus* improved bobwhite nest success in 2014, 2015, or 2016.
3. Treatment with *Extinguish Plus* did not improve the percent of female bobwhites with broods or the mean brood size per female.

Based on the results of our research, the use of *Extinguish Plus* to reduce RIFA did not lead to greater bobwhite relative abundance. It is possible that our results are related to factors other than those that we researched, such as predator abundance and vegetation succession differences between the treated and nontreated areas of the APCNWR during our study.

Additional research or a longer term study of the effects of large-scale RIFA treatment on bobwhites would be beneficial to either strengthen or oppose the conclusions of our study. Unlike other proposed remedies to the quail decline (e.g., habitat restoration), aerial RIFA treatment is relatively inexpensive and easy to implement. If such treatment proves effective at increasing bobwhite abundance, these methods will provide wildlife managers a tool that could increase their chances of slowing, stopping, or reversing the quail decline.

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IMPACTS OF RED IMPORTED FIRE ANTS ON NORTHERN BOBWHITE NEST SURVIVAL

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ABSTRACT

Invasive species are a large management issue because of extensive environmental and economic damage. The red imported fire ant (RIFA, *Solenopsis invicta*) is an invasive species of growing concern in wildlife management in the United States because of its increasing distribution, difficulty to suppress, and aggressive predation on native invertebrates, herpetofauna, birds, and small mammals. Managers of the northern bobwhite (*Colinus virginianus*) have questioned the direct impact of RIFA on bobwhite nest success, particularly the factors that might influence the level of nest predation. We hypothesized that RIFA predation on northern bobwhite would vary by location and correlate with drier weather conditions. To test our hypothesis we analyzed bobwhite nest data gathered from 3 properties in the southeastern United States. The nest data are part of a larger research effort on bobwhites, collected by Tall Timbers Research Station and the Albany Quail Project using radiotelemetry from 1992 to 2015. Over these 23 years we tracked bobwhites and located nests ($n = 3{,}207$) daily to determine nest fate (success or failure) based on field sign and evidence attributed to specific causes of mortality. We used the nest-survival model in Program MARK to estimate nest survival. Average nest survival varied annually for the Albany and Tall Timbers study areas, respectively. The overall effect of RIFAs on nest survival was generally small, with an average annual loss in Albany of 5.13% (range = 0–15.59%) and 2.17% in Tall Timbers (range = 0–5.83%), but in some years was as high as 15.6%. Greater losses occurred late in the breeding season when it was typically drier and the loss rate in general was higher on the drier of the 2 study sites. Despite the relatively small direct impact on nesting success demonstrated, indirect effects of RIFAs on bobwhite populations are poorly understood at present. Quantifying the influence of indirect factors, such as soil type and habitat disturbance, on RIFA abundance and the subsequent impact on bobwhites, will provide additional insight to the ecological interaction with a highly pervasive and expanding invasive species and help inform management options.

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Key words: drought, gamebird management, invasive species, KBDI, Keetch–Byram Drought Index, nest predation, quail

One of the greatest conservation threats worldwide is the spread of invasive species, given their large economic and environmental cost to individual flora and fauna and to the integrity of ecosystems as a whole (Pyšek and Richardson 2010). In the United States alone, the estimated economic loss from invasive species is >US $1.1 billion annually (Allen et al. 2004). Beyond the economic impact of invasive species, they are a leading cause of animal extinction (Clavero and García-Berthou 2005) and have been linked to decreasing biodiversity and impairment of ecosystem services worldwide (Pejchar and Mooney 2009, Pyšek and

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Richardson 2010). Preventing the establishment or slowing the spread of invasive species, evaluating their effects on ecosystems, and determining appropriate management responses to invasion are high priorities for wildlife managers globally (Lowry et al. 2013).

An invasive species of particular concern in North America is the red imported fire ant (RIFA(s), *Solenopsis invicta*). Red imported fire ants are a prime example of an invasive species benefitting from changing land-use practices and anthropogenic disturbance (e.g., pastures, mowed areas near roadways, disking; Tschinkel 1988, Camilo and Phillips 1990, Plowes et al. 2007). Native to South America, this species was introduced into the United States during the 1930s or 1940s (Callcott 2002). The widespread availability of highly disturbed land enabled RIFA's rapid population expansion in the southern United States, despite a 1953 U.S. Department of Agriculture quarantine intended to slow its spread. The species has become established in >128 million ha in 13 southern U.S. states and Puerto Rico, as well as in other Caribbean islands, Mexico, Australia, and China (Morrison et al. 2004, Zhang et al. 2007). Under current climatic conditions RIFA has the potential to continue expanding its U.S. distribution northward within southern states and in the Pacific Coast region to Washington State (Korzukhin et al. 2001, Morrison et al. 2004), with even further northward expansions possible under a 21st century climate-warming scenario (Morrison et al. 2005). This historical establishment and continued expansion of RIFA is of urgent conservation concern. Red imported fire ants reach high densities, are highly aggressive, and are omnivorous, giving them potential to impact species ranging from agricultural crops (Jetter et al. 2002), to invertebrates, to vertebrates including herpetofauna, mammals, and birds (Allen et al. 2004). Among vertebrate wildlife species, ground-nesting birds in particular may be at risk of negative population-level effects of RIFA predation (Wojcik et al. 2001, Allen et al. 2004).

A ground-nesting species of frequent concern is the northern bobwhite (*Colinus virginianus;* hereafter, bobwhite [Allen et al. 2004]). Even prior to RIFA invasions, native fire ants (*S. geminata*) were known as a source of bobwhite mortality and nest loss during pipping (Stoddard 1931, Travis 1938). The accidental introduction and rampant spread of RIFAs stimulated research on their potential effects on bobwhite and other wildlife (Johnson 1961, Simpson 1976). Bobwhites are negatively affected by RIFAs via direct nest predation (Myers et al. 2014), reduced chick survival through harassment (Allen et al. 2004), and competition for similar food resources (Williamson et al. 2002). In the case of nest predation, the majority of studies indicate that the pipping stage, or soon afterward, is when chicks are most vulnerable to RIFA predation (Mueller et al. 1999, Staller et al. 2005). This observation holds true for other taxonomic groups that have an altricial–precocial spectrum as well. For instance, both altricial (e.g., American alligator [*Alligator mississippiensis*], Reagan et al. 2000) and precocial (e.g., loggerhead turtle [*Caretta caretta*; Allen et al. 2001] reptiles are affected by RIFA.

Recent studies have compared impacts of polygyne vs. monogyne varieties of imported fire ants (Macom and Porter 1996) and evaluated their response to specific management actions (Forbes et al. 2002). Studies have also documented a severe impact of RIFA on bobwhite in the Southwest, particularly in Texas (Mueller et al. 1999, Allen et al. 2004). The impact seen in Texas is largely attributed to the high density of polygyne RIFAs, where colonies have multiple queens and ≥3 RIFA density than is observed in monogyne RIFAs (Macom and Porter 1996). High RIFA density in Texas could explain the high predation rates on bobwhite in those areas (Allen et al. 2004). Polygyne RIFAs are found in the Southeast but at much lower densities than are present in Texas (Porter 1992).

Although RIFAs can negatively affect individual bobwhite and have the potential to contribute to landscape-scale population declines, considerable uncertainty remains about long-term average rates of RIFA-caused mortality and the amount and causes of spatial and temporal variability in these mortality rates. This uncertainty reduces the ability of managers to identify the conditions (i.e., when and where) under which RIFA effects on bobwhite warrant higher concern. At within-region scales, RIFA occurrence and activity are affected by site disturbance history, hydrology, and climate (Porter and Tschinkel 1987, Tschinkel 1988). There are likely other factors that influence RIFA that are, as of yet, not well-quantified. Spatial variation in density and other factors presumably could produce variation in RIFA impacts on bobwhite but there has been little work assessing the relative effects of disturbance history and other factors on such variation. Anecdotal evidence suggests that RIFA foraging behavior is altered by moisture or lack thereof, such that severe droughts can trigger more aggressive foraging behavior because the ants are unimpeded by rainfall events and at the same time are driven to seek sources of moisture (Porter and Tschinkel 1987, LeBrun et al. 2012). However, potential interannual variation in RIFA-caused mortality rates, such as differences between drought and nondrought years, are poorly understood because assessing such temporal variation requires long-term data sets.

Given the need for better understanding of variability in RIFA impacts on bobwhite, our goal was to quantify the impact of RIFA on bobwhite nest survival using a long-term data set from the Albany Quail Project and Tall Timbers Research Station and Land Conservancy and to evaluate impacts of RIFAs in relation to geographic location, year, and season. Based upon this goal and the existing literature, we hypothesized that RIFA predation 1) would vary significantly by location and 2) would increase during drier periods. We expected our results to have direct relevance to numerous bobwhite managers in our study region, where bobwhite hunting and conservation are a focus of many landowners, and to help improve understanding of RIFA–bobwhite interactions throughout their area of overlap in the United States.

STUDY AREA

The Albany Quail Project study site was composed of 2 adjoining private bobwhite hunting plantations in Baker and Dougherty counties of southwest Georgia. One 8,094-ha property served as the headquarters of the project, the second property was 4,400 ha with a similar history and management program to the first (Sisson et al. 2009, Sisson and Stribling 2009). The 2 properties were embedded in a 120,000-ha landscape of similar properties. The sites consisted of small basal area (9.2–13.8 m^2/ha), old-field pine forests (80%) in an open pine–grassland structure maintained through commercial thinning, prescribed fire (50–70% of the areas burned each year), with small fallow fields throughout the area. The majority of the timber was longleaf pine (*Pinus palustris*) and slash pine (*P. elliottii*), with scattered hardwoods such as live oak (*Quercus virginiana*), southern red oak (*Q. falcata*), and water oak (*Q. nigra*). Herbaceous cover was predominantly warm season grasses, such as broomsedge (*Andropogon* sp.), annual broad-leaved forbs, and legumes. Both properties were converted to agricultural fields in the 1800s; however, after agriculture was abandoned in the 1900s these lands were seeded back to pine and native vegetation maintained by prescribed fire. The average growing season for the duration of this study was 15 March to 31 November (varies with weather), with an average temperature of 76° F (24° C). The average annual precipitation for Albany was 127 cm, with an average of approximately 74 cm during the bobwhite breeding season.

Topography on both Albany properties was relatively flat with little to no hardwood drains. Quail estimates for these sites in recent years have averaged approximately 5 birds/ha (Sisson et al. 2009). For further site descriptions, see Terhune et al. (2007).

Tall Timbers was located in Leon County, Florida, embedded in an approximately 161,874-ha landscape of other bobwhite management properties. Like the Albany properties, Tall Timbers was largely old field vegetation and consisted of 1,568 ha of old-field pine forests (66%) of loblolly pine (*P. taeda*) and shortleaf pine (*P. echinata*), interspersed with hardwood drains and hammocks (12%) and small fallow fields (13%; see Palmer et al. 2012). Pine forests maintained an open pine–grassland structure through prescribed fire (50% burned annually). Herbaceous ground cover was a mix of warm season grasses, legumes, and forbs (Hammond 2001). Quail estimates for this site in recent years have averaged approximately 3.75 birds/ha. The average growing season was 15 March to 31 October (varies with weather), with an average temperature of 78° F (26° C) and an average annual precipitation for Tall Timbers of 158 cm, with an average of approximately 91 cm during the bobwhite breeding season.

Soils on the Albany sites were of the Orangeburg–Lucy–Grady and Norfolk–Wagram–Grady soil associations, which were predominantly sandy-loam textured soils with moderate permeability and low natural fertility (Palmer et al. 2012). Soils on Tall Timbers are of the Fuquay–Orangeburg–Faceville soil association, characterized by well-drained, moderately fertile, fine-loam soils with varying amounts of sand and clay (Palmer et al. 2012). The Orangeburg series was common in both Albany and Tall Timbers sites but otherwise there were no shared soil families, meaning soils between sites varied in characteristics such as horizonation, mineral composition, and permeability.

METHODS

From 1992 to 2015, we captured bobwhites during October and November (autumn trapping period), January (winter trapping, only on Tall Timbers), and March–April (spring trapping period) using confusion-style funnel traps baited with milo and/or cracked corn (Stoddard 1931). We covered traps with brush (e.g., fresh-cut pine boughs) to minimize stress on captured birds and to conceal them from avian predators. We classified captured bobwhites by age and sex, weighed and tagged all birds, and radiotagged a subset of birds weighing $\geq$132 g with a 6-g necklace-style radiotransmitter equipped with an activity switch (Holohil Systems Ltd., Carp, Ontario, Canada). We used necklace-style transmitters because they do not influence body mass dynamics or physiology of captive birds (Corteville 1998, Hernandez et al. 2004) and their effect on survival of bobwhites is negligible (Palmer and Wellendorf 2007, Terhune et al. 2007).

We located radiotagged individuals $\geq$3 times weekly during the breeding season (1 Apr–1 Oct) using the homing method (White and Garrott 1990, Kenward 2001). We approached birds to within 25 m to minimize location and vegetation classification errors and we recorded locations using ArcView® software (Environmental Systems Research Institute, Inc., Redlands, CA, USA).

Inactive birds, determined via an activity switch, were assumed to be incubating hens if observed in the same area on 2 consecutive days. We approached inactive hens and marked their location with flagging tape at a distance of 3–10 m to monitor the fate of the nest daily from a distance $>$15 m. We used a Global Positioning System (Garmin V Plus; Garmin Ltd., Olathe, KS, USA) and/or aerial imagery to delineate and archive nest locations. We counted the number of eggs in a nest when the incubating hen was off the nest. We monitored nests daily and determined daily fate categorized as abandoned, successful, or unsuccessful. An unsuccessful nest was any nest in which $\geq$1 egg was destroyed and the adult bird did not return to incubate the remaining clutch. An abandoned nest was one in which the hen did not complete incubation and all eggs were still intact. Abandoned nests (typically research induced) were excluded from analyses. This caused no bias in the RIFA analysis because nests observed with RIFA were classified as a failure, not an abandoned nest. A successful nest included those in which $\geq$1 egg hatched. We identified nest predators by video camera (when available) or by sign or tracks left at the nest. Despite known biases associated with assigning nest mortality by sign or tracks, video-surveillance research showed that RIFA depredations almost always were correctly classified by field staff based on presence of RIFA (Staller et al. 2005).

Statistical Analysis

We estimated daily survival rate (DSR) for bobwhite nests and evaluated competing models explaining variation in nest survival using the nest survival model in Program MARK (White and Burnham 1999). We modeled our binomially distributed data (nest fate = 1 if failed and 0 if successful) with a user-defined, logit-link function while simultaneously considering the effects of time (day of year and year effect; linear and quadratic time trends; T and TT), year (modeled as individual groups: 1992–2015), group (predation type: red-imported fire ants, other), and site (Albany, Tall Timbers). For our data, we standardized 15 April as Day 1 and numbered nest observations sequentially thereafter until Day 191 (10 Sep), the final day of nesting activity during our study (see Dinsmore et al. 2002, Rotella et al. 2004). We coded each individual nest with the following pieces of required information to input into Program MARK (see White and Burnham 1999, Dinsmore et al. 2002): 1) the day the nest was found (k), 2) the last day the nest was checked and known alive (l), 3) the last day the nest was checked (m), and 4) the nest fate (f). Additionally, we used indicator variables to assign individual nest encounters to group-specific covariates as outlined above (i.e., year, group, site, and treatment type). We incorporated a measure of dryness into nest survival analysis using the Keetch–Byram Drought Index (KBDI), whereby KBDI values of 0–200 indicate substantial soil moisture, KBDI values of 200–400 indicate beginning stages of drought and moderate dryness, KBDI values of 400–600 indicate drought conditions, and KBDI values of 600–800 indicate severe drought and extremely dry conditions.

We used an information-theoretic approach (Akaike 1973, Anderson et al. 2000, Anderson and Burnham 2002) to evaluate the set of candidate models with the best model determined by Akaike's Information Criterion adjusted for small sample bias (AIC_c; Wedderburn 1974, Anderson and Burnham 2002). We considered the model with the smallest AIC_c value the best given the data and considered the relative plausibility of each model via Akaike weights (w_i; Anderson et al. 2000, Anderson and Burnham 2002), where the best approximating model in the candidate set has the greatest Akaike weight. When appropriate, we used model-averaging (Akaike 1974, 1978; Anderson and Burnham 2002) to obtain daily survival and estimated nest survival as the product of DSR across the 23-day incubation period. To derive additional inference and render direct covariate-specific comparison, we report beta coefficients, their standard errors and 95% confidence intervals, and effect size for variables of interest (e.g., site, treatment); and, for comparison with other studies, we report the derived estimates of DSR (with associated 95% CI).

RESULTS

Between 1992 and 2015, we found 3,207 nests on Albany ($n = 1{,}822$) and Tall Timbers Research Station ($n = 1{,}385$) study sites, with an average of 134 nests found each year (range = 35–307; Table 1). Average annual loss of nests to RIFA on Albany sites was 5.13% (range = 0–15.59%) and on Tall Timbers was 2.18% (range = 0–5.38%). Three models received support in explaining the variation in nest survival but one model (an interaction between site and predator-type) was overwhelmingly supported more than the others (Table 2).

The most-supported model included site and non-RIFA predators and the top 3 models all included non-RIFA predators. Comparatively, the models ranked next best (which incorporated RIFAs) received no support, suggesting that RIFA explained relatively little variation in nest survival compared with other nest predators (Table 2). The inclusion of year was not supported and explained very little variation in our data with the exception of 2 years on the Albany sites ($\beta_{1993} = -0.606$; 95% CI = -1.199, -0.014 and $\beta_{2007} = -0.640$; 95% CI = -1.218, -0.063) and 2 years on the Tall Timbers site ($\beta_{2011} = -0.464$; 95% CI = -0.861, -0.066 and $\beta_{2013} = -0.491$; 95% CI = -0.913, -0.070); these 4 years had the lowest nest survival in their respective sites (Fig. 1).

In the models incorporating an effect of RIFA, variation in nest survival was best explained by site and a linear time trend (Table 2). Red imported fire ants depredated more nests on Albany sites (DSR = 0.996, SE = 0.001) compared with Tall Timbers sites (DSR = 0.998, SE = 0.001) for all years combined (Fig. 2) and DSR for those nests depredated by RIFAs was higher than those depredated by all other nest predators combined. Red imported fire ants decreased daily nest survival and survival decreased linearly with the progression of the season ($\beta_T = -0.002$; 95% CI = -0.003, $-<0.001$; $\beta_{RIFAs} = -0.721$; 95% CI = -0.929 -0.513) such that nest survival was lower at the end of the season compared with early in the nesting season. The KBDI influenced nest survival in a curvilinear relationship, such that lower DSRs were observed at low KBDI (<200) levels and high KBDI (>400) levels ($\beta_{KBDI} = -0.170$; 95% CI = -0.290, -0.050; $\beta_{KBDI\wedge 2} = -0.438$; 95% CI = -0.630, -0.250; Fig. 3). Keetch–Byram Drought Index levels were on average higher on Albany sites compared with Tall Timbers; high levels of KBDI (≥ 425 and ≥ 370) in Albany and Tall Timbers, respectively, were associated with increased nest failure (Fig. 4).

DISCUSSION

Our results supported the first hypothesis that RIFA predation would vary by location. Bobwhite nest loss due to RIFA fluctuated between geographic locations, with the Albany sites having more nest mortality than Tall Timbers (Fig. 2). Our results indicate that the direct impact of RIFA predation on bobwhite nest survival generally is low at our 2 study sites, with only 4% average loss for the sites combined. However, predation was greater in some years and on some areas of the study region. The reason for the disparity between nest mortality by site in our study is unclear but could be due to subtle vegetation differences related to either or both soil characteristics and local climate affecting RIFA densities and/or their impact on bobwhite nests. For

Table 1. Northern bobwhite nest success at Albany, Georgia, and Tall Timbers Research Station (TTRS), Florida, USA, study sites during 1992–2015.

	Albany			TTRS			
Year	n(succ)[a]	n(dep)[b]	n(total-PL)[c]	n(succ)	n(dep)	n(total-TTRS)[d]	Total
1992	33	30	63				63
1993	10	25	35				35
1994	53	38	91				91
1995	41	31	72				72
1996	47	37	84				84
1997	56	35	91				91
1998	54	50	104				104
1999	92	88	180	12	17	29	209
2000	124	91	215	46	46	92	307
2001	64	38	102	31	35	66	168
2002	30	43	73	86	40	126	199
2003	49	41	90	34	35	69	159
2004	35	33	68	42	22	64	132
2005	28	28	56	41	16	57	113
2006	24	31	55	59	38	97	152
2007	23	28	51	34	22	56	107
2008	33	37	70	63	40	103	173
2009	25	13	38	64	39	103	141
2010	21	27	48	37	30	67	115
2011	30	19	49	38	56	94	143
2012	37	23	60	59	28	87	147
2013	35	18	53	29	44	73	126
2014	12	10	22	41	53	94	116
2015	31	21	52	62	46	108	160
TOTAL	987	835	1,822	778	607	1,385	3,207

[a] No. of successful northern bobwhite nests.

[b] No. of depredated northern bobwhite nests.

[c] Total no. of nests in the Albany study area.

[d] Total no. of nests in the TTRS study area.

Table 2. Model selection results for analysis of nest survival of northern bobwhites on Albany, Georgia, and Tall Timbers Research Station, Florida, USA, during 1992–2015.

Model[a]	ΔAIC_c[b]	w_i[c]	Model L	K[d]	Deviance
S + Site + non-RIFA + Site × non-RIFA	0.0	0.998	1.000	4	10,085.9
S + Site + non-RIFA	13.2	0.001	0.001	3	10,101.1
S + non-RIFA	14.3	0.001	0.001	2	10,104.1
S + T + RIFA	2,585.2	0.000	0.000	3	12,673.1
S + T + TT + RIFA	2,585.8	0.000	0.000	4	12,671.7
S + Site + T + RIFA	2,587.2	0.000	0.000	4	12,673.0
S + RIFA + KDBI + KBDI × KBDI	2,589.2	0.000	0.000	4	12,675.0
S + RIFA + KBDI	2,590.0	0.000	0.000	3	12,677.9
S + RIFA	2,591.0	0.000	0.000	3	12,678.9
S + Site + RIFA	2,591.1	0.000	0.000	3	12,679.0
S + Site + RIFA + Site × RIFA	2,592.9	0.000	0.000	4	12,678.8
S + KBDI	2,594.0	0.000	0.000	2	12,683.9
S + T	2,621.5	0.000	0.000	2	12,711.4
S + T + TT	2,622.5	0.000	0.000	3	12,710.4
S.	2,626.3	0.000	0.000	1	12,718.2
S + Site	2,628.3	0.000	0.000	2	12,718.2

[a] S = ?; Non-RIFA = all predations recorded besides RIFA (RIFA = red imported fire ants predation); T = Linear within-year time trend; TT = quadratic trend; KDBI= Keetch–Byram Drought Index.

[b] Change in AIC_c.

[c] AIC_c weight.

[d] The no. of free parameters in the model.

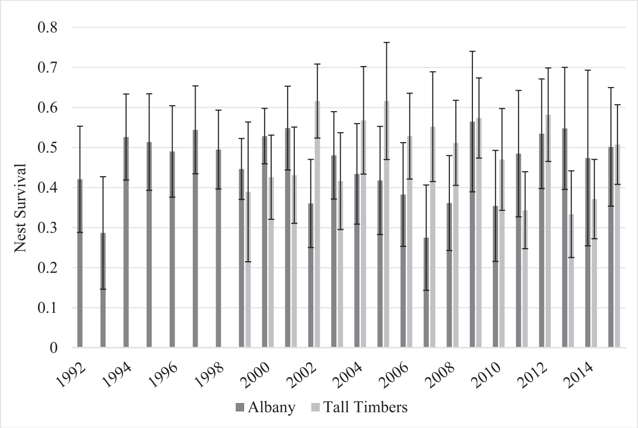

Fig. 1. Northern bobwhite nest survival for Albany and Tall Timbers Research Station, Florida, USA, for 1992–2015.

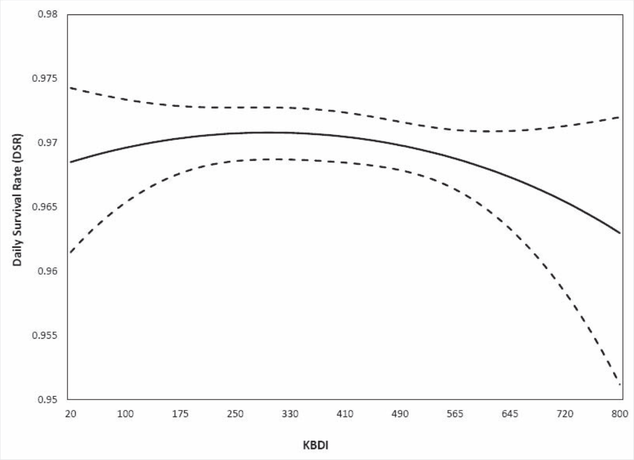

Fig. 3. Predicted daily survival rate for northern bobwhite nests relative to the Keetch–Byram Drought Index (KBDI) on Albany and Tall Timbers study sites, Florida, USA, during 1992–2015.

example, the Tall Timbers site has more fertile soils and receives approximately 25–38 cm of annual rainfall more than the Albany sites, which may influence vegetation conditions depending on timing and amount of rainfall in a given year.

The nest mortality rates we observed are similar to previous studies in the Southeast, which recorded 5–12% bobwhite nest loss at pipping (Johnson 1961). We observed variation in nest mortality attributed to RIFA among sites, with a 5.13% loss rate in Albany versus only a 2.18% loss rate at Tall Timbers (Fig. 1). Such small loss rates may not be biologically significant; however, in years when nest loss to RIFA is as high as 15.6%, the loss is biologically meaningful. Notably, 20 years prior to the start of our study in the Albany study area, Simpson (1976) found <1% loss to RIFA. Several possibilities exist for the temporal discrepancies between studies, including differing techniques (nest search vs. telemetry), disparate vegetation conditions or management regimes, or possibly differing RIFA densities. Red imported fire ants had only recently infested southern Georgia at that time (Allen et al. 2000), so it is possible there were fewer colonies during Simpson's study; however, we have no direct data to confirm this. Studies have shown a pattern of bobwhite decline following fire ant invasion in Texas (Allen et al. 1995) as well as in the Southeast (Allen et al. 2000) but did not document a similar relationship in Georgia (Allen et al. 2000). Our studies in Albany likewise have not documented declining populations during these years; bobwhite populations are currently as large as or larger than they have been in 50 years (Sisson and Stribling 2009). This stability could be due to long-term management regimes and abundant food sources for bobwhites. As such, high bobwhite densities may mitigate the overall impact of RIFA on bobwhite populations but additional research is warranted on low-density sites.

Although variation existed in RIFA predation between sites, there was no difference in the non-RIFA mortality agents of nests across sites. There was, however,

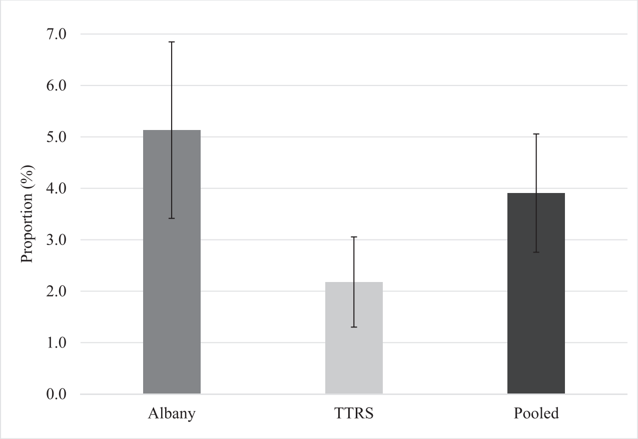

Fig. 2. Average annual proportion of northern bobwhite nests depredated by red imported fire ants on Albany, Tall Timbers Research Station (TTRS), and all sites pooled in Florida, USA for 1992–2015.

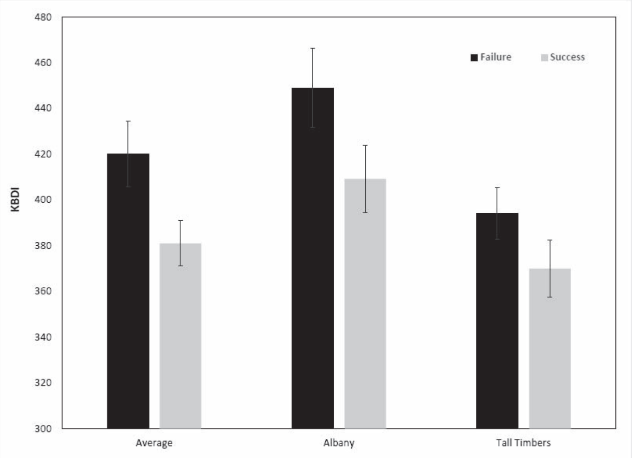

Fig. 4. Northern bobwhite nest survival relative to the Keetch–Byram Drought Index (KBDI) on Albany and Tall Timbers study sites, Florida, USA, during 1992–2015.

a notable difference in the daily survival rates (DSRs) of nests, with those predated by RIFA having higher DSRs than those predated by non-RIFA predators on all sites. Our finding is expected because RIFA typically depredate nests at the pipping stage, thus mainly affecting nests that had survived nearly to hatching. This is significant because it means a greater time investment by the bobwhite parents and when the nest is lost they have less time in the breeding season to renest.

With the exception of fallow field percentage, both study sites employ similar management regimes (i.e., prescribed fire, disking) and land-use history (managed similarly for $\geq$40yr). Therefore, the lack of variation in other nest mortality agents was not surprising but presumably factors outside of the management regimes must be driving variation in RIFA impacts. Major differences between sites include soil type and climate. Albany sites have sandy soils, while Tall Timbers has loamy, more clay-based soils. However, there is little information on whether RIFA colonization and densities are related to soil types and this could be influencing the variation we observed in our results. Some studies have found no evidence that soil type affects RIFA (Wangberg et al. 1980, Porter et al. 1991); whereas, others suggest that a relationship exists, with sandier soils having slightly higher RIFA abundance than silty or loamy soils (Ali et al. 1986). Interestingly, Ali et al. (1986) conducted their research in an intensive agricultural setting, which may be similar to more intensive fallow field management in the Albany sites compared with the Tall Timbers site in our study. Explicitly testing whether intensive soil disturbance, through farming or fallow field management, in relation to other environmental factors, may expose site-specific conditions facilitating RIFA distribution.

Climate, precipitation, or level of dryness is known to impact RIFA foraging behavior and/or nest depredation rates (LeBrun et al. 2012). Average annual rainfall on Tall Timbers (158 cm) is greater than on Albany (127 cm) sites and Tall Timbers receives 25–38 cm more rainfall than Albany. Albany sites and soils are more drought-prone and also experienced higher rates of depredation at pipping by RIFA (Fig. 2).

The temporal variation we observed supported our second hypothesis that RIFA predation would correlate with warmer, drier climate conditions. Across sites, nest survival decreased relative to time of season and KBDI (level of dryness), which is linked to higher temperatures and less precipitation typical later in the breeding season compared with earlier in the season. Past research has found a connection between higher RIFA predation rates and climate, particularly during drought conditions (LeBrun et al. 2012). Drought conditions and level of dryness (measured by KBDI in our study) was an indicator of nest survival, such that at low levels ($<$200) and high levels ($>$400) daily survival rate of nests was low compared with normal levels (200–400 KBDI). It is unclear from our study why this is the case, especially when KBDI is low. We expect, however, that when KBDI levels are low nest depredations by mammals might increase as a result of favorable scent conditions due to increased moisture (Conover 2007). When KBDI is high and drought conditions persist, lower nest survival and specific loss to RIFA increased in our study (Fig. 4). Notably, annual variation in nest survival in our data only occurred in 4 of 23 years on each study site. During 3 of these 4 years, the KDBI was higher than the long-term average and considered to indicate drought conditions based on the Palmer Drought Index, particularly during the breeding season in 1993 (KBDI = 545) and 2007 (KBDI = 524) for the Albany sites, and 2011(KBDI = 480) and 2013 (KBDI = 245) for Tall Timbers. These years also had the lowest bobwhite nest survival for their respective sites (Fig. 1). In light of declining nest survival throughout the breeding season and KBDI being higher in August and September, the potential impact of RIFA on the late hatch may be biologically relevant, especially during drought years, given that the late hatch can be a purported boon to overall productivity, autumn recruitment, and population growth (T. M. Terhune, unpublished data).

The proportion of direct RIFA nest depredation in our study was similar to previous studies (Johnson 1961, Simpson 1976) but the significant variation of impact between sites and magnitude of nest loss to RIFA relative to KBDI has not been explicitly evaluated. Human disturbance has been linked to RIFA invasions (Tschinkel 1988, King and Tschinkel 2008) and habitat management may influence their expansion. Management practices, such as prescribed burning, have been examined for connections to RIFA density (Forbes et al. 2002), yet their impacts are poorly documented. Examining indirect variables such as geographic location, soil type, climate, and species interactions in relation to bobwhite management practices could reveal connections to RIFA presence or absence and density at a given location. These indirect effects could have negative effects on bobwhite populations, especially if RIFA expansion and mound densities continue to escalate. For example, the hispid cotton rat (*Sigmodon hispidus*) is an important bottom-level prey species, serving as an alternate prey species for predators of bobwhite (Harris 2011). Red imported fire ants depredate cotton rat young, and past studies have recorded alteration in cotton rat behavior and even habitat use when RIFA invade an area (Pedersen et al. 2003). More research is needed to quantify these relationships, which could in turn shed light on indirect influences RIFAs have on bobwhites and other ground-nesting birds. Understanding how environmental factors and land-use practices impact RIFA density, expansion, and behavior will provide valuable knowledge for land managers to determine whether RIFA treatment regimens are necessary for bobwhite conservation.

MANAGEMENT IMPLICATIONS

Although the overall impact of RIFA predation on bobwhite nest survival is low, we found evidence suggesting that these impacts can be site-specific and magnified during drought conditions, especially in conjunction with the late hatch. Therefore, during most years control of RIFA is unnecessary. However, the impacts of RIFA are more problematic on some sites when soils and climatic conditions are more drought-prone. In these scenarios, RIFA removal may be an option for land managers trying to improve bobwhite populations but more research is warranted to determine whether removal results in lower RIFA abundance and moderates their impact on nest survival. At the moment, the potential cost of directly reducing RIFA populations by treating large acreages may be unrealistic and the potential deleterious impacts on other species are uncertain. Thus, until more information is available, the best management strategy for bobwhite populations is mitigating nest loss to RIFA by increasing productivity with management methods (e.g., vegetation management and other common practices) that have been rigorously tested and validated.

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LANDSCAPE FEATURES AFFECTING NORTHERN BOBWHITE PREDATOR-SPECIFIC NEST FAILURES IN SOUTHEASTERN USA

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ABSTRACT

Nest predation is a critical component in avian productivity and typically is the leading cause of nest failure for most birds. Several landscape features are thought to drive the behavioral interaction between northern bobwhite (*Colinus virginianus;* e.g., nest placement) and their predators (e.g., search methods for food acquisition). In order to understand habitat characteristics influencing predation, we studied bobwhite nests using 24-hour near-infrared video cameras. We monitored 675 bobwhite nests with cameras on 3 properties in northern Florida and southern Georgia, USA, during 2000–2006. To test the association between nest failures and specific failure causes with landscape structure, we calculated a suite of landscape metrics and examined these at 3 spatial scales (3.1 ha, 19.6 ha, and 50.3 ha). We found increased probability of nest success with greater proportions of, and proximity to, fallow and annually disked fields at larger scales (50.3 ha), but we found no landscape metrics to be important predictors of bobwhite nest failures at small scales ($<$20 ha). Fallow and disked fields may provide alternative prey items (e.g., rodents) important in buffering nest predation. Relative to meso-mammal predation, we observed increases in proportion of the landscape in field to be related to lower incidental nest failures at the smallest scale (3.1 ha). Nests closer to feed lines were more likely depredated by meso-mammals than ants at the 2 larger spatial scales. Interestingly, the fate of a nest was independent of the fate of neighboring nests, suggesting bobwhite nest predation may be primarily incidental.

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Key words: *Colinus virginianus,* Florida, Georgia, landscape metrics, nest camera, nest predation, northern bobwhite

Predation is a process that relies on the interactions among predators, prey, and the habitat where they coexist. Nest predation is considered the leading cause of nest failure for most avian species (Ricklefs 1969). Effective management to enhance breeding success of an avian species requires accurate identification of the predators responsible for failures, as well as knowledge of predator and prey distribution, abundance, diversity, and habitat use. Nest predation is likely to be in part the result of incidental encounters of predators with nests (Vickery et al. 1992, Jones et al. 2004). Therefore, management that reduces the probability of these interactions may result in

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increased reproductive success. Frequently, predator control is used to mitigate nest losses for many gamebirds and imperiled bird species; however, many conflicting results exist about its effectiveness to enhance avian reproductive success and abundance (Côté and Sutherland 1997, Newton 1998). Northern bobwhites (*Colinus virginianus*) are a declining grassland- and early successional-dependent species. Bobwhites are vulnerable to predation because they nest on the ground with large clutches and relatively long nest-exposure periods. Habitat management has been considered an effective tool at enhancing bobwhite populations based on the premise that predator populations can be manipulated indirectly through habitat modifications (Errington 1934, Rollins and Carroll 2001). This nonlethal method has been suggested as the first tool that should be implemented to offset predation losses (Rollins and Carroll 2001). In order to increase bobwhite reproductive output, biologists need to first understand the complex relationship among the predators, bobwhite nests, and the habitats, which leads to increased interactions between the nests and the predators.

Although nest success in northern bobwhites is well-studied, much less is understood linking predation and specific nest failures with habitat associations (Staller et al. 2002), and specifically what spatial scales might be most important to bobwhite reproductive success (Roseberry and Klimstra 1984, Taylor et al. 1999b, White et al. 2005). Radiotelemetry technology has enhanced our understanding of bobwhite nest selection; yet identification of the predators responsible for nest predation events is rarely known because signs at the nest may be misleading (Lariviere 1999, Staller et al. 2005, Lusk et al. 2006). Traditional studies of bobwhite nesting relative to habitat features have focused its influence on nest site selection or nest success (Taylor et al. 1999a, b; White et al. 2005; Collins et al. 2009). Only one study to date has examined the specific predator species responsible for bobwhite nest failures and their interactions with habitat characteristics (Staller et al. 2002). Advances in camera technology have enabled biologists to accurately identify nest predators and has become a popular tool in studying avian nest predation (Pietz and Granfors 2000, Staller et al. 2005). This technology can assist in identifying nest predators and might help link nest predation to habitat associations across the landscape.

Common bobwhite nest predators include raccoons (*Procyon lotor*), nine-banded armadillos (*Dasypus novemcinctus*), opossums (*Didelphis marsupialis*), bobcats (*Lynx rufus*), red and gray fox (*Vulpes vulpes* and *Urocyon cinereoargenteus*), coyotes (*Canis latrans*), skunks (*Mephitis mephitis*), snakes (*Elaphe* spp. and *Lampropeltis getula*), and fire ants (*Solenopsis* spp.; Hernandez et al. 1997, Fies and Puckett 2000, Staller et al. 2005). These predators have broad diet and habitat needs and they are thought to opportunistically feed on nests. Therefore, understanding how features on the landscape determine predator behaviors, such as foraging, has substantial value in managing not just bobwhites, but also grassland wildlife (Kuehl and Clark 2002).

Habitat edges may serve as travel corridors for many wildlife species, particularly medium-sized mammals (Heske et al. 1999, Chalfoun et al. 2002, Kuehl and Clark 2002, Phillips et al. 2003). However, some studies contradict the role linear edges may play in mammalian predator movement (Pasitschniak-Arts et al. 1998). Ecotones and other edges are frequently found to be preferred for snake species, particularly in northern regions (Weatherhead and Charland 1985). Edges may be important to predators, particularly where habitat patches are small with relatively little "core" area to be searched (Temple 1986). For some species, such as fox, activity is greater in smaller patches (Sovada et al. 2000) and is likely the result of a fragmented landscape with many edges that enable the predator to search the area with greater efficiency. Edges may attract avian nesting but these abrupt transition zones may serve as ecological traps where birds are more vulnerable to predation because of surrounding, low quality habitat.

Although many bobwhite predators are generalists, research is lacking on the habitat composition and configuration preferences that might influence the ability of these predators to find avian nests (Phillips et al. 2003). These generalist meso-mammals frequently exploit a variety of habitats including mixed habitats with forested area, shrub land, old fields, agricultural areas, wetlands, and suburban areas (Reid et al. 2006). However, some meso-mammalian predators were found to prefer specific habitat cover types in the Prairie Pothole Region of North America (Phillips et al. 2003). In addition, edge use was dependent upon the types of surrounding land cover, with wetlands being more attractive edges for meso-mammals (Phillips et al. 2003). Snake species utilize a variety of habitats including wooded and shrub areas with both hardwood and pine forests and wetland edges. Within the snake community, used habitats often are different even among closely related species. For example, corn snakes (*Elaphe guttata*) most often use upland pine areas, whereas gray rat snakes (*Elaphe spiloides*) are most often found in hardwood drains (Stapleton 2005). Thus, wildlife managers could benefit in understanding whether specific habitat composition and configuration of land-cover types might increase predation risk to avian nests by certain predator guilds.

The objectives of this study were to determine the landscape composition and configuration features important to nest fate and the specific predators responsible for nest failures across 3 different spatial scales. This was conducted by coupling radiotelemetry, nest camera technology, Geographical Information Systems (GIS), and spatial analysis tools. The findings of this study provide insight on spatial scales at which the nest predation process is occurring, underlying spatial relationships to the predation process, and potential management that may minimize nest predation.

STUDY AREA

We studied bobwhite nesting at 3 sites in southern Georgia and northern Florida during 2000–2006. Tall

Timbers Research Station and Land Conservancy, Inc. (Leon County, FL; 84°13′35″W, 30°39′39″N) and Pebble Hill Plantation (Thomas and Grady County, GA; 84°5′48″W, 30°46′13″N) are located in Red Hills physiographic region are. Pinebloom Plantation (Baker County, GA; 31°24′42″N, 84°22′45″W) is located in the Upper Coastal Plain physiographic region. Detailed site description for the Red Hills sites can be found in Staller et al. (2005), and for Pinebloom in Sisson et al. (2000, 2009). Sites are dominated by loblolly (*Pinus taeda*) and shortleaf pine (*P. echinata*) with associated "old-field" ground cover vegetation and areas of longleaf pine (*P. palustris*) with associated wiregrass (*Aristida stricta*) ground cover. All 3 sites use frequent fire (1–3-yr rotations), disking, roller-chopping, and mowing to maintain an open, low-density pine forest structure. Hardwood drains, hammocks, fallow fields, and wetlands are interspersed across the landscape. On the greater landscape, the adjacent land to Pinebloom Plantation includes some row-crop agriculture predominantly for cotton and peanuts. Supplemental feeding of bobwhites occurred on all 3 properties. Every 2–3 weeks, sorghum was spread at a rate of approximately 6 bushels/1.6 km on specified trails (feed lines). In addition to supplemental feeding, nest predator reduction was occurring on sites in some years from 1 March to 30 September. No predator reduction occurred on either site in 2000, but in 2001–2003 predators were reduced on the eastern half of Pinebloom Plantation and at Pebble Hill Plantation while Tall Timbers Research Station and Pinebloom West did not receive any predator reduction. From 2004 to 2006, the predator reduction efforts were switched and Tall Timbers Research Station and Pinebloom West had predator reduction while the other 2 sites served as controls. Detailed information about predator removal can be found in Ellis-Felege et al. (2012).

METHODS

Bobwhite Nesting

On each study site, we captured bobwhites each year between January and April, 2000–2006, using baited funnel traps (Stoddard 1931). We classified captured bobwhites by age and sex, and fitted each with 6.5g (~4% body-weight) collar-style radiotransmitters (Staller et al. 2005). All trapping, handling, and marking followed approved protocols by the University of Georgia Institutional Animal Care and Use Committee permits A2004-10109-c1 and A3437-0. Using radiotelemetry homing techniques (White and Garrott 1990), we located bobwhites ≥5 days/week to monitor nesting behavior between 15 April and 1 October of each year. Bobwhites found in the same location on 2 consecutive days and did not have the mortality sensor activated were assumed nesting. We placed flagging near the nest site location so the nest could be relocated when the incubating bobwhite was off the nest. We recorded the nest location into a geodatabase using GIS and ArcGIS software (Environmental Systems Research Institute, Inc., Redlands, CA, USA). We were able to find nests and begin monitoring within the first few days of incubation so nests were approximately the same age when located (Taylor et al. 1999b).

When the incubating bobwhite was away from the nest as determined by telemetry, we installed a continuous-recording, near-infrared camera (Furhman Diversified, Seabrook, TX, USA) at the nest. We placed the small camera with a near-infrared (950-nm) lighting source approximately 1–1.5 m from the nest opening (Staller et al. 2005). We camouflaged the cameras using surrounding vegetation. Cameras and lighting sources were linked via a 25-m cable to very high standard (VHS) recorders and 225-reserve capacity, deep-cycle battery. We modified the recorders to operate at one-third speed, allowing an 8-hour tape to last 24 hours. We replaced tapes and batteries daily. We checked nests daily via telemetry until failure or hatch, thus minimizing errors in failure dates. We viewed videos to confirm fate of the nest and identify the nest predator if the nest failed. We categorized nests first as successful (i.e., hatched ≥1 egg) or failed. From camera monitoring, we further classified failed nests as failed due to meso-mammals, snakes, ants, and other factors (e.g., incidental predators or bobwhites killed away from the nest). We did not explore predation patterns relative to partial clutch loss and individual egg mortality but rather only those where no eggs hatched from a nest.

Land Cover

We digitized land-cover types at 1:1,500-m scale using 1999 Digital Orthophoto Quarter Quardrangles in ARCMAP v9.2 (Environmental Systems Research Institute, Inc.). To validate land-cover types and to update polygons for the study years (2000–2006), we used first-hand knowledge of the study area, remote imagery, and handheld GPS locations from the field. We delineated 10 land-cover types. These included pine (i.e., open pine savannah), planted pine (i.e., densely planted pine stands), agriculture (i.e., row crops), ragweed and fallow fields, hardwood drains, roads, feed lines, wetland, open water, other (i.e., predominantly urban).

Landscape Metrics

We were most interested in spatial relationships of nest fates relative to the composition of the landscape at different scales, proximity of specific landscape features to the nest, and amount of edge near nests at the different scales. We constructed circular buffers around each nest site with radii of 100 m (3.14 ha), 250 m (19.6 ha), and 400 m (50.3 ha). We selected buffer sizes based upon the variety of home range sizes in the predator community with home ranges <20 ha for armadillos and snakes (Layne and Glover 1977, Stapleton 2005), approximately ≥50 ha for raccoons (Chamberlain et al. 2003a) and at the site-level spatial scale for bobcats and coyotes (Chamberlain et al. 2003b). We chose not to use larger radii because of substantial overlap among nests that would have resulted in nonindependence in our data and required us to remove nearby nests, thus decreasing sample sizes.

These scales encompassed bobwhite home ranges on the study areas (Sisson et al. 2000, Wellendorf and Palmer 2009), were representative of home ranges in other areas of Georgia (Parnell et al. 2001), and were comparable to previous studies examining bobwhite nesting relative to landscape characteristics (Staller et al. 2002, White et al. 2005). We intersected each buffer size with the land-cover layer of the study areas using ARCMAP intersect tools. Within each buffer, we calculated percent composition of the habitat cover types. We calculated Euclidean distance between nests to landscape features of interest (e.g., roads, feedlines, hardwood drains). Using FRAGSTATS (Version 3.3; McGarigal et al. 2002), we used a moving-window analysis to calculate edge density at each scale (total length of edge in the landscape divided by total area of landscape and did not include edges from perimeter of the buffer). We focused on edge density because edges are thought to be primary travel corridors for predators. We extracted these values to the nest point using the Spatial Analyst Tool "Extract Values to Point" in ARCMAP.

Statistical Analysis

First, we assessed nest failures (e.g., success or fail) relative to specific landscape metrics using a logistic regression in SAS (Version 9.3; SAS Institute, Inc., Cary, NC, USA). We initially examined models at each of the 3 spatial scales to determine which models were most important at the individual scales. To avoid collinearity, we conducted Pearson correlations on all pairs of predictor variables. We considered $r^2 > 0.3$ to be a conservative estimate of correlated variables (Moore and McCabe 1993) and thus did not use them in the same regression model. We selected one of the metrics we hypothesized might be most important in the interaction of predators with the nest. We selected 9 metrics to use as predictors variables including percent of hardwood composition within each buffer, percent of wetland composition within each buffer, percent of annually disked fields composition within each buffer, edge density at each buffer size, distance to hardwoods, distance to fields, distance to wetlands, distance to roads, and distance to feed lines. Rather than run all combinations of models, we explored *a priori* models of individual parameters of interest, combinations of models that we thought were biologically important, and a global model (all uncorrelated parameters of interest). Biologically important combinations included models about both distance to and composition size to a particular habitat type (specifically, wetland or hardwood drain habitats), additive model of distance metrics to all features of interest given the importance to edges, and composition-only models that include overall composition of fields, wetlands, and hardwood drains. We examined $\hat{c}$ of the global model to determine whether the data were over-dispersed where a $\hat{c} > 1.0$ represents overdispersion (Lebreton et al. 1992). We ran a Hosmer–Lemeshow goodness-of-fit test in SAS on the global model, where an adequate fit is observed if the $P > 0.05$ (Hosmer and Lemeshow 1989). We found no overdispersion, so we used model selection approaches (Akaike's Information Criterion adjusted for small sample sizes; AIC_c) to determine the models that described the data best (Burnham and Anderson 2002). The best-fitting models at each scale and a global model of scale-independent metrics were then used in a subsequent multiscale analysis to determine which scale, if any, described the probability of nest failures best. Model-averaged estimates from the entire candidate model set were calculated for the coefficients of the predictor variables (Burnham and Anderson 2002, Anderson 2008). Model-averaged odds ratios were calculated for the parameter estimates and for interpretation, scaled to biologically significant values important for management at each of the 3 spatial scales and for a multiscale model using the top 2 models from each individual scale.

Second, conditioned on nest failure, we examined the specific cause of nest failure (e.g., meso-mammal [baseline], snake, ants, and other) relative to landscape metrics using a multinomial model at the 3 spatial scales. We selected uncorrelated metrics as described above in the nest success models, and evaluated goodness-of-fit using a likelihood ratio test, where adequate fit is observed if $P > 0.05$ (Menard 2002). Models were evaluated at each of the 3 spatial scales using AIC_c model-selection approaches described above for the logistic models (Burnham and Anderson 2002). We present model-averaged estimates for each of the coefficients of the predictor variables with odds ratios scaled to biologically relevant values important to management for interpretation and provide summary information for the parameters in the top models.

Additionally, we examined the residuals of the top regression models and calculated Moran's I to determine if any spatial structure was not accounted for by the predictor variables (Overmars et al. 2003) using Program SPATIAL ANALYSIS in Macroecology (SAM; version 3.1, http://www.ecoevol.ufg.br/sam/; Rangel et al. 2006). We also explored spatial structure within our response variables by plotting correlograms and examining average Moran's I to determine whether any spatial structure might exist in the underlying nest failure process. A Moran's I-value near 0 indicates no spatial autocorrelation where values near 1 and –1 indicate clustering and randomness, respectively (Cliff and Ord 1981).

RESULTS

During the 7-year study, cameras were installed at 675 bobwhite nests (Felege 2010). We excluded 29 nests from subsequent analysis because these nests were abandoned as a result of research activities (primarily a result of camera installation). Of the remaining 646 nests, 394 nests (61.0%) succeeded and 252 (39.0%) failed. We examined ultimate causes of nest failure and not individual egg mortality or any partial predation events. The specific failures were attributed to meso-mammals ($n = 92$ nests: 36.5% of failures), snakes ($n = 67$ nests: 26.6% of failures), ants ($n = 28$ nests: 11.1% of failures), and other incidental causes ($n = 30$: 11.9% of failed nests). At 35 nests (13.9% of failed nests), exact failure causes could

Table 1. Model selection using Akaike's Information Criterion (AIC_c) weights of the top 2 models from each of the 3 spatial scales and a global model of uncorrelated metrics incorporated into a multiscale model examining the relationship between the probability of northern bobwhite nest failure and landscape metrics in northern Florida and southern Georgia, USA, 2000–2006. For the smaller scales, the models were both scale-independent metrics for proximity and the same models described the data best.

Model	K	AIC_c	ΔAIC_c	Weight
Int + Field Distance + Field Composition (50.3 ha)	3	914.52	0.00	0.352
Int + Field distance + Field Composition (50.3 ha) + Wetland Distance + Hardwood Distance	5	915.03	0.50	0.274
Int + Hardwood Distance	2	915.05	0.53	0.270
Int + Wetland Distance + Hardwood Distance	3	916.96	2.44	0.104

not be determined from the camera footage because dense vegetation often limited visibility for small species (e.g., snakes). Failures classified as unknowns were not meso-mammals predators because these predators were easily identified even in thick vegetation but were suspected to be snakes (Staller et al. 2005). Unknown failures were included in the logistic failure models only. More detailed descriptions of annual and by study area nest failures can be found in Ellis-Felege et al. (2012).

Nest Failures Relative to Landscape Features

Global models at all scales demonstrated adequate fit ($P > 0.05$) and no overdispersion was observed in the data ($\hat{c} = 1.01$). The best-fitting models included distance to hardwood drains only and an additive model of distance to hardwoods and to fields for both the 3.1-ha and the 19.6-ha models. However, no predictors strongly influenced the probability of nest failures at the 2 smaller scales (3.1-ha and 19.6-ha scales). Model-averaged parameter estimates for these predictors had estimates close to 0 and 95% confidence intervals encompassing 0 with no strong trend for a positive or negative relationship with nest failures. At the 50.3-ha scale, the best-fitting model describing the probability of nest failures was percent field composition and distance to fields ($AIC_w = 0.455$). Within the 50.3-ha buffered area, the probability of nest failure was 1.6 times less likely with each 10% increase in field composition. Probability of nest failure was 1.1 times less likely with each 50-m increase in distance between the nest and the field.

The top 2 models at each scale, and the global model, were then examined as a candidate model set to determine which scale best described the probability of failure. The top model was an additive model of percent field composition at the 50.3-ha scale and distance to fields (Table 1). This model had 40.5% of the model weight and was 1.3 times more likely than the next best-fitting model of distance to hardwood patches. At the 50.3-ha scale, the probability of nest failure was 1.7 less likely with every 10% increase in field composition (Table 2). For every 50-m increase in proximity to fields, the probability of nest failure was 1.1 times less likely (Table 2). Successful nests, on average, were farther from field edges and wetlands, but closer to hardwood drains (Table 3).

We found no spatial autocorrelation in the residuals of the overall top model for the probability of nest failure (Moran's $I_{avg} = -0.008$; Fig. 1); therefore, no modification to the modeling structure was necessary (Cliff and Ord 1981). We examined the correlogram for the response variable of nest success or failure with respect to the proximity of nests from one another and found overall no spatial pattern (Moran's $I_{avg} = -0.009$). We hypothesized that predation at neighboring nests would be more likely related to nests within the same year so we further examined the spatial relationship of the response variable by year. Generally, we found very little spatial relationship in nest fate relative to the nest fate of neighboring nests (Fig. 2), except for 2002 and 2005 where there appeared to be slight clustering in the fate of nests within 200 m of one another (Moran's $I = 0.36$ and 0.42, respectively).

Specific Failure Causes Relative to Landscape Features

Global models at each scale indicated adequate fit for the multinomial models examining landscape metrics on specific failure causes ($P > 0.05$). Predator-specific failure causes were influenced differently by landscape metrics at the 3.1-ha scale compared with the 2 larger scales. Distance to fields was in top models at all 3 scales. Percentage of fields described the data best at the 3.1-ha and 19.6-ha scales, whereas the best-fitting models included percentage of hardwoods. Most of the model-averaged parameter estimates were near 0 and had broad

Table 2. Model-averaged parameter estimates for coefficients of the landscape metrics potentially influencing the probability of northern bobwhite nest failures in northern Florida and southern Georgia, USA, 2000–2006.

Parameter	Estimate	SE	95% LCI	95% UCI	Unit scalar	Scaled odds ratio	Scaled LCI	95% CI UCI
Intercept	−0.0481	0.40251	−0.837	0.6121				
Distance to fields	−0.0021	0.00094	−0.004	−0.0006	50	0.8998	0.8208	0.9719
Field composition (50.3 ha)	−0.0488	0.01917	−0.0864	−0.0174	10	0.6138	0.4215	0.8405
Distance to wetlands	−0.0001	0.00028	−0.0007	0.0003	50	0.9936	0.9666	1.0166
Distance to hardwoods	0.0004	0.00018	0	0.0007	50	1.0181	1.0000	1.0336

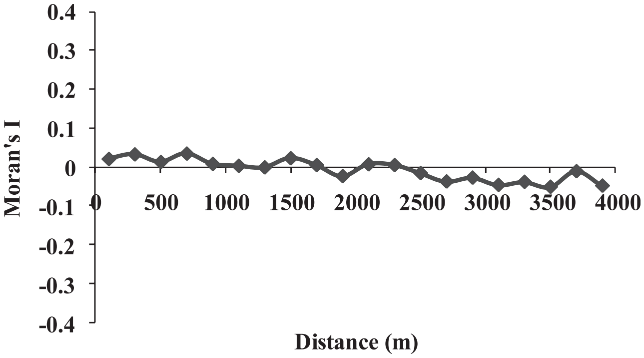

Fig. 1. Correlogram of Moran's *I* for the spatial structure of the residuals of the top model (Percent Field Composition at 50.3-ha scale + Distance to Fields) for the probability of northern bobwhite nest failure during 2000–2006 in southern Georgia and northern Florida, USA. Values of Moran's *I* close to 0 indicate no spatial autocorrelation.

95% confidence intervals that encompassed 0. When we examined models from each spatial scale, we found the smallest scale predictor of percentage of field composition best described the probability of predator-specific failure (Table 4). At the 3.1-ha scale, for every 10% increase in field composition, other predation events were 2.2 times less likely than meso-mammal predation events (Table 5). On average, higher proportions of field within the smallest scale buffer were associated with ant predation (Table 6). With every 10% increase in field composition, we found ant predation to be 1.3 times more likely than meso-mammal predation events and snake predation events to be 1.1 times more likely than meso-mammal events at the smallest scale (Table 5). For every 50-m increase in proximity to feed lines, ant depredations were 1.04 times more likely than meso-mammal predation events (Table 5). Meaning, on average, most meso-mammal predation events were closer to feed lines than any other nest failures (Table 6). We also found that each 10% increase in hardwood composition at the 50.3-ha scale increased the probability of ant predation by 1.3 times that of meso-mammals (Table 5).

We examined spatial structure in the response variable by comparing meso-mammals first with all other failure causes collectively (i.e., snakes, ants, and other). Then, we compared meso-mammals with each of the other 3 failure causes individually. Similar to the success–failure model, we observed little spatial autocorrelations among the nest failure cause of neighboring nests when meso-mammals were compared with all other failure causes collectively or individually (Moran's $I_{\text{avg}} < 0.2$).

DISCUSSION

We found that the relationship between fate of bobwhite nests and landscape attributes was dependent upon the spatial scale at which the landscape metrics were evaluated. At the small scale (<20 ha), metrics were not particularly informative for explaining nest fate and models best describing the failure process were scale-independent metrics of proximity. Failures at nests can result from a large suite of different predator species, each with their own foraging methods and relationship with the habitat features we explored. These smaller scales correspond to some of the predominant predator species, such as armadillos (Layne and Glover 1977) and gray rat snakes (Stapleton 2005), which have home ranges <20 ha. However, many of the predators, such as raccoons (Urban 1970, Chamberlain et al. 2003a), have large home ranges that exceed 20 ha. In fact, top predators such as bobcats and coyotes have home ranges that can exceed even our largest scale (Chamberlain et al. 2003b).

At larger scales (>50 ha), we found the greater the percent field composition the more likely the nest was to succeed. Our results suggest that the nest predation process is likely operating at scales related to the larger predator home-range sizes. Annually disked fields, ragweed fields, and fallow fields provide sources of food to bobwhites that would be valuable during the nesting season (Klimstra and Roseberry 1975). Having these habitats readily available may minimize bobwhite foraging time or number of daily foraging trips that may leave a nest more vulnerable to predation. Perhaps more importantly, though, is the role of cotton rats (*Sigmodon hispidus*). Cotton rats are a common alternative prey item for many bobwhite predators (Schoch 2003) and work done on our study area demonstrated fields are preferred habitat for this species at our study sites (Hannon 2006). Thus, a greater abundance of cotton rats might equate to a greater abundance of alternative prey options for predators. Nesting studies examining alternative prey have found increased availability of alternative prey to be correlated with greater nesting success for waterfowl (Byers 1974, Weller 1979, Crabtree and Wolfe 1988, Vander Lee et al. 1999). Although this might be directly related to alternative prey availability, this might also be a function of diversion of predators to habitats for foraging where bobwhites do not commonly nest. Potentially there is an interactive effect of alternative prey and foraging diversion.

Examining predator-specific failures, we found that at the smallest scale (3.1 ha) field composition was also important. At the smallest scale, percent field composition

Table 3. Summary statistics of landscape metrics in top models relative to successful and depredated bobwhite nests in northern Florida and southern Georgia, USA, 2000–2006.

	Distance to field (m)			% Field composition (50.3 ha)			Distance to wetland (m)			Distance to hardwood drain (m)		
Nest fate	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Success	122.51	0.00	473.84	7.04	0.00	24.45	417.88	0.00	1,701.07	329.99	0.00	2,442.16
Fail	112.43	0.00	470.06	6.29	0.00	21.96	389.41	0.00	1,364.57	439.72	0.00	2,174.38

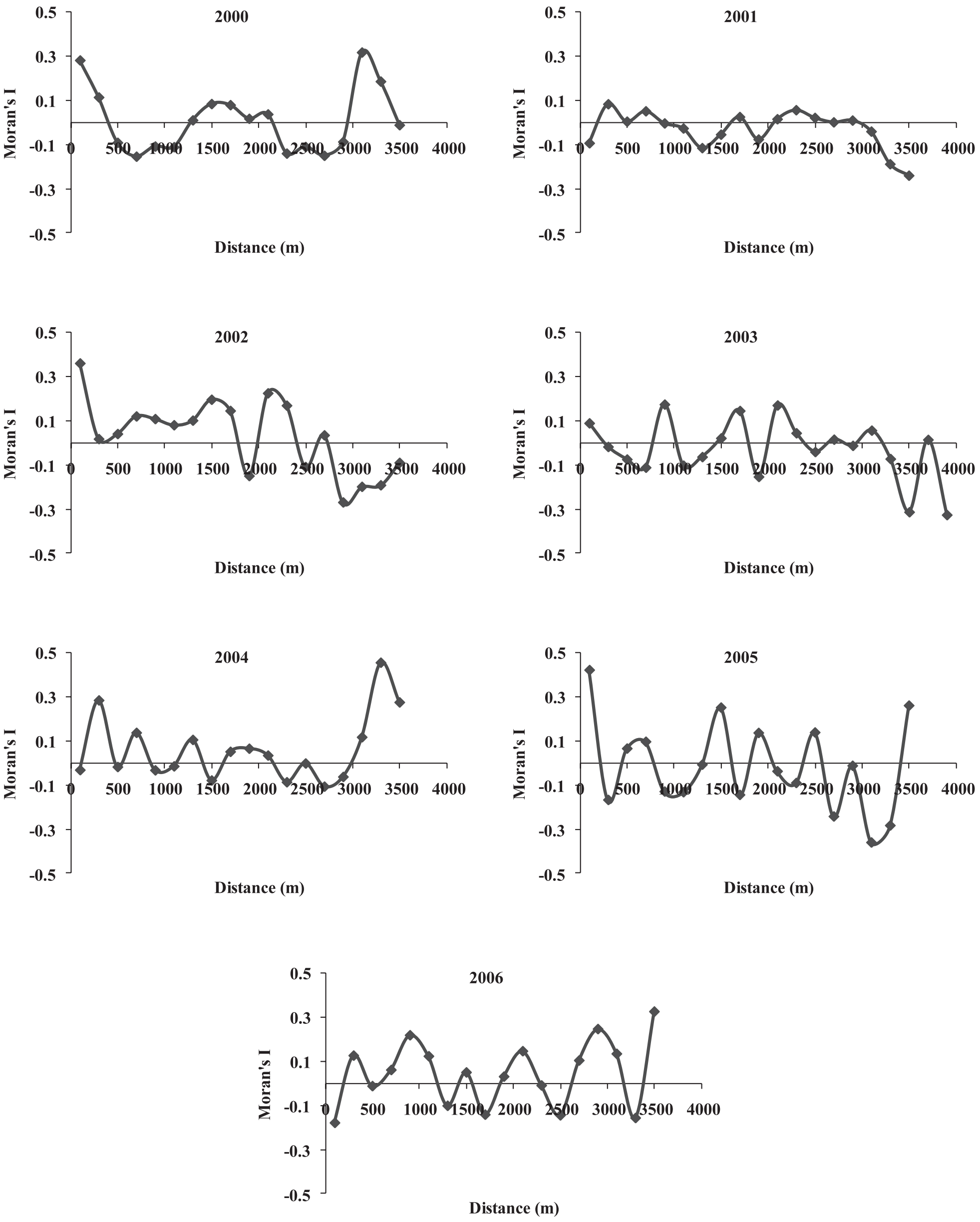

Fig. 2. Correlogram of Moran's *I* for the binary response variable of success or failure of northern bobwhite nests during 2000–2006 in southern Georgia and northern Florida, USA, showing the spatial autocorrelation between nests, where *I*-values close to 0 indicate no relationship in nest fate to the fate of neighboring nests.

described the data best for incidental failures compared with meso-mammals predation events at the nest. Many of the incidental failure causes were the result of mortality of the incubating bobwhite while it was away from the nest. From a management perspective, there is still the potential for renesting when the nest fails because of predation by meso-mammals as long as the bobwhite survives.

Distance to feed lines was important in ant depredations relative to meso-mammals at the 2 larger scales. There is relatively little understood about the how fire ants interact with habitat management. Habitat disturbances such as burning and mowing appear to enhance ant populations (Williamson et al. 2002) but supplemental feeding practices have not been examined relative to ants. The red imported fire ants could be attracted to seeds and are known to disperse seeds of native plant species (Zettler et al. 2001, Stuble et al. 2009); however, we found on average most ant predation events were farther from feed lines than other predators. Other studies have documented trends that supplemental feed lines attract bobcats (Godbois et al. 2004) and avian predators (Haines et al. 2004) and may be playing a role in our findings.

We observed no differences between landscape features that strongly influence snake predation differently from meso-mammals. Only percent field composition appeared to slightly increase snake predation relative to meso-mammals at our smallest scale, but decreased snake predation relative to meso-mammals at the 19.6-ha scale.

Table 4. Model selection using Akaike's Information Criterion (AIC_c) weights of the top 2 models from each of the 4 spatial scales incorporated into a multiscale model examining the relationship between the probability of specific failure causes (meso-mammals, snakes, ants, and other) at northern bobwhite nests and landscape metrics in northern Florida and southern Georgia, USA, 2000–2006. Scale-independent metrics for proximity to feed lines described the predator-specific failure causes best at the 2 larger spatial scales (19.6 ha and 50.3 ha).

Model	AIC_c	ΔAIC_c	Weight
Int + Field composition (3.1 ha)	549.75	0.00	0.700
Int + Field composition (3.1 ha) + Feed line distance	551.97	2.22	0.231
Int + Feed line distance	556.30	6.55	0.026
Int + Field composition (19.6 ha)	556.57	6.82	0.023
Int + Hardwood composition (50.3 ha)	556.91	7.16	0.019

These predator guilds are generalists and have very broad habitat and diet requirements as well as potentially species-specific habitat preferences. By pooling snakes into one category, we may have obscured habitat characteristics influential to specific snake species. For example, gray rat snakes in the area of this study frequently used hardwoods and wetlands more than corn snakes, which predominantly used upland pine habitat (Stapleton 2005). Furthermore, kingsnakes may be more likely found in the uplands than rat snakes (Ernst and Ernst 2003). Staller et al. (2002) recommended bobwhite nesting cover be promoted away from drain edges to reduce snake predation but gray rat snakes were the predominant snake species in that study. However, in our study, this would only partially mitigate snake predation. On one of our study sites, Pinebloom, kingsnakes were the primary snake predators, whereas both species of rat snakes were the common snake predators in the Red Hills Region. Unfortunately, it was not always possible to identify snakes to species from our camera data. Thus, future work focusing on species-specific failures may yet identify habitats or landscape structures related to increased risk of failure.

We observed that fate of an individual nest appeared to be spatially independent of the fate of neighboring nests during most years. Although it may seem intuitive that predators would return to an area where they previously had success, research on learning and foraging theory suggests otherwise (Real 1994). For example, this could be the result of predators selecting among patches with varying resource availability. An alternative explanation could be that predators are trying to search an area efficiently; therefore, they might not return to an area previously exploited because they have already searched it. Angelstam (1986) also found predators did not appear to develop a memory for the location of artificial nests. For generalist predators like those in our study, it may be that random foraging modified by some selection of habitats with large amounts of alternative food sources, such as fields, is the most efficient search method because predators have broad dietary requirements that can easily be met within this landscape. Thus, predation on bobwhite nests is probably incidental, as has been found for other grassland bird nests functioning as incidental prey for striped skunk (Vickery et al. 1992).

Years (2002, 2005) for which we observed a slight spatial pattern in the nest fate were years when production was very high, and many bobwhites on our study areas had second nests. We observed renests by individual birds to be fairly close to one another. Thus, the relationship between proximity and nest fate may have been less an artifact of the predation process but instead related to the success of an individual bird. In other words, bobwhites

Table 5. Model-averaged parameter estimates for the coefficients of landscape metrics influencing the probability of northern bobwhite nest failures due to specific predators (meso-mammals, snakes, ants, and other failures) in northern Florida and southern Georgia, USA, 2000–2006.

Parameter	Estimate	SE	LCI	UCI	Unit scalar	Scaled odds ratio	Scaled LCI	95% UCI
Intercept[a]	−0.787	0.270	−1.317	−0.257				
Intercept[b]	−1.502	0.317	−2.124	−0.881				
Intercept[c]	−0.396	0.211	−0.810	0.018				
Field composition (3.1 ha)[a]	−0.077	0.037	−0.150	−0.005	10	0.462	0.224	0.953
Field composition (3.1 ha)[b]	0.026	0.019	−0.010	0.063	10	1.302	0.905	1.874
Field composition (3.1 ha)[c]	0.010	0.015	−0.020	0.040	10	1.105	0.817	1.493
Feedline distance[a]	0.000	0.000	−0.001	0.001	50	1.002	0.959	1.047
Feedline distance[b]	0.001	0.000	0.000	0.001	50	1.036	0.999	1.073
Feedline distance[c]	0.000	0.000	0.000	0.000	50	1.001	0.999	1.004
Field composition (19.6 ha)[a]	−0.058	0.040	−0.137	0.021	10	0.559	0.254	1.232
Field composition (19.6 ha)[b]	0.028	0.032	−0.035	0.091	10	1.323	0.708	2.473
Field composition (19.6 ha)[c]	−0.018	0.027	−0.070	0.035	10	0.839	0.497	1.417
Hardwood composition (50.3 ha)[a]	−0.003	0.020	−0.042	0.036	10	0.967	0.654	1.428
Hardwood composition (50.3 ha)[b]	0.030	0.017	−0.004	0.063	10	1.343	0.961	1.878
Hardwood composition (50.3 ha)[c]	−0.005	0.015	−0.034	0.025	10	0.955	0.709	1.286

[a] Other nest failure causes relative to meso-mammals depredations.

[b] Nest failures due to ants relative to meso-mammals depredations.

[c] Nest failures due to snakes relative to meso-mammal depredations.

Table 6. Mean and range of landscape metrics at bobwhite nests delineated by nest failure cause and successful nests in northern Florida and southern Georgia, USA, 2000–2006.

	% Field composition (3.1 ha)			% Field composition (19.6 ha)			R Hardwood composition (50.3 ha)			Distance to feed line (m)		
Nest fate	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Meso-mammal	7.15	0.00	53.48	6.75	0.00	26.84	8.46	0.00	53.04	373.70	0.00	1,999.04
Snake	8.24	0.00	42.94	6.10	0.00	22.03	7.94	0.00	44.41	403.05	0.00	1,510.99
Ant	10.62	0.00	39.87	7.98	0.00	27.45	12.86	0.00	39.25	624.26	0.00	2,043.01
Other	2.91	0.00	19.81	4.90	0.00	29.18	8.08	0.00	36.94	388.05	0.77	1,909.00
Successful	6.86	0.00	80.97	7.21	0.00	37.00	9.54	0.00	55.28	414.13	0.00	2,101.86

with successful first nests were more likely to have successful second nests or vice versa. Microhabitat features selected by the bobwhite may have influenced the fate of the nest. Amount of litter cover, vegetation height, and presence of specific plant species may camouflage some nests better than others (Taylor et al. 1999a) and certain bobwhites might be better at microhabitat selection for nest sites than are other bobwhites.

Studies have found edges to be important (Heske et al. 1999, Chalfoun et al. 2002, Kuehl and Clark 2002, Phillips et al. 2003) but we did not find edge density or distance to edges to strongly influence the probability of nest failures except for field edges. Although models at smaller scales indicated distance to edges of hardwoods described the data best from our model-selection approaches, this predictor was no more or less likely to influence nest fate. Distance to field edge, however, was negatively related to the success of a nest and may have been related to attributes of the field that attracted predators to these sources of abundant alternative prey. Therefore, increased probability of nest encounter by a predator would be more likely. These results seem to contradict our findings of increased field composition benefiting bobwhite nesting. There is a definite tradeoff but, in most cases, the percentage of these fallow or annually disked ragweed fields on the larger landscapes is generally small. For example, our observed ranges were 0–25% field composition at the 50.3-ha scale.

The impact of cameras at nests is always a concern for interpretations of nest predation and bird behaviors. Work by Staller et al. (2005) on a subset of the bobwhite nesting data presented here found no impacts of cameras on nesting birds. However, because it is difficult to determine predator fates without cameras (Pietz and Gransfors 2000, Staller et al. 2005, Rader et al. 2007) and whether specific predators may be attracted or deterred by the camera setups, it is largely unknown what specific impacts, if any, the cameras may have on predator-nesting bird interactions. Thus, our interpretations are based upon the predators we observed at the nests from the cameras and may have unknown biases.

MANAGEMENT IMPLICATIONS

Our results suggest that creation of early successional, fallow fields, which is often done to create bobwhite brood habitat, also benefits nesting and therefore should be encouraged. It is important to note that our maximum field composition was 25% and therefore model results should not be extrapolated to landscapes composed of higher fractions of field habitat. Our results also suggest that feed lines along roads might impact nesting bobwhites by creating additional food resources for mammals or attracting mammals to those areas. The tradeoff in management is likely to be in the timing of when managers stop providing feed after winter.

One caveat of our study is that we monitored bobwhites in a habitat that is managed to sustain high bobwhite densities; therefore, influences of many potential factors that could drive the predation process may have been diluted relative to their effects in more degraded habitats typical of the modern landscape. Future work should focus on extending our study toward understanding predation in areas with intensive agriculture, forestry, and more fragmented habitats. A better understanding of landscape-mediated predation pressure in these areas may offer additional management alternatives for biologists to minimize predator–bobwhite interactions during the breeding season.

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HABITAT, CLIMATE, AND RAPTORS AS FACTORS IN THE NORTHERN BOBWHITE DECLINE: A MULTI-SCALE ANALYSIS

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ABSTRACT

Landscape-level processes such as habitat loss and fragmentation are primarily responsible for the declines in northern bobwhite (*Colinus virginianus*). These landscape processes generally occur at a scale beyond that of traditional quail studies and may involve not only habitat loss and fragmentation but also broad-scale changes in climate trends and predation risk. However, reductions in usable space and changes in habitat configuration at smaller scales may also reduce population viability. It is therefore imperative to study relationships to bobwhite populations at multiple scales. The objective of our research is to quantify to what extent habitat loss and fragmentation, climate, and predators are affecting quail populations at multiple scales within Texas. Our study area will include the Rolling Plains and Rio Grande Plains ecoregions, which are historic strongholds of bobwhite, though each has seen recent declines. We will examine the relative contributions of 3 general factors (habitat, climate, and predators) on quail populations at multiple scales (ranch, route-level, and landscape). Specifically, these factors include total habitat amount, degree of fragmentation, raptor relative abundance, temperature, and precipitation. We will obtain data from multiple sources to determine quail trends (Breeding Bird Survey and ranch-level data) and relate habitat trends (National Land Cover Database and Texas Ecological Systems Classification Project), raptor abundance (Breeding Bird Survey), and climate factors (PRISM) within a multiple linear regression framework. This study will provide an understanding of 1) to what degree habitat loss and fragmentation are affecting quail populations on Texas rangelands, 2) how other factors such as climate and predators may be compounding these effects, and 3) how these relationships vary at multiple scales.

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Key words: landscape, scale, habitat fragmentation, climate, raptors

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EFFECT OF MESO-MAMMAL NEST PREDATOR ACTIVITY ON NORTHERN BOBWHITE NEST SUCCESS

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ABSTRACT

Perceived changes in predator-prey dynamics along with documented declines of northern bobwhite (*Colinus virginianus*) have created a renewed interest from biologists and managers about the role meso-mammals play in shaping bobwhite population trajectories. As part of a larger effort to understand this predator-prey relationship, we evaluated meso-mammal activity on sites where bobwhite demographic data was simultaneously being collected via radio- telemetry. During 1999–2006 we conducted 66 meso-mammal activity surveys using scent stations on 16 sites in 3 southeastern states (Florida, Georgia, and Alabama). We calculated an index of meso-mammal activity (PI), for each site, as the average number of station visits per night by raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), nine-banded armadillos (*Dasypus novemcinctus*), bobcats (*Lynx rufus*) and foxes (*Vulpes vulpes*, *Urocyon cinereoargenteus*). We collected bobwhite reproductive information on 2,940 nests ($\bar{x} = 45$/site, SE = 2.98) from a total of 4,379 radio-tagged bobwhites ($\bar{x} = 67$/site, SE = 3.81). The average PI for all sites combined was 0.13 (range = 0.03-0.38, SE = 0.01). Nesting success on the sites ranged from 0.29 to 0.72 and averaged 0.52 (SE = 0.01). We used a mixed effects logistic regression model including site as a random effect and observed a negative relationship between the PI and nesting success ($\beta = -1.53 \pm 0.72$ SE). Our results suggest that meso-mammal activity affects bobwhite nest success, thus, predator management may be warranted at times on some sites to maximize productivity. Future research and modeling efforts should explore the impacts of meso-mammal activity on population growth rates and stability, especially in varying spatial contexts.

Citation: Warnell, D. B., W. E. Palmer, D. C. Sisson, T. M. Terhune II, and J. A. Martin. 2017. Effect of meso-mammal nest predator activity on northern bobwhite nest success. National Quail Symposium Proceedings 8:356.

Key words: *Colinus virginianus*, index of activity, meso-mammal, nesting success, northern bobwhite, predation management, predator-prey, radio-telemetry

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EVALUATION OF POPULATION INDICES AND ESTIMATORS FOR SCALED QUAIL IN THE ROLLING PLAINS OF TEXAS

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ABSTRACT

Accurate and precise population indices and estimators are important to gain reliable knowledge and make appropriate management decisions. Indices and estimators for scaled quail (*Callipepla squamata*), however, have not been evaluated thoroughly. Our objectives are to compare relationships among 8 years of roadside counts, spring call counts, and mark-recapture data obtained from the Rolling Plains Quail Research Ranch in Fisher County, TX, USA. Furthermore, we assess the efficacy of distance-based helicopter surveys as a method for scaled quail density estimates as compared to mark-recapture estimates for 2016–2017.

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Key words: scaled quail, *Callipepla squamata,* population indices, mark-recapture, density estimates

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POPULATION TRENDS AND A REVISED MANAGEMENT PLAN FOR QUAIL IN CALIFORNIA

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ABSTRACT

California supports a diversity of habitats suitable for mountain quail (*Oreortyx pictus*), California quail (*Callipepla californica*), and Gambel's quail (*Callipepla gambelii*). These three species require different habitats for foraging, nesting and brood-rearing, and over-winter survival, yet most published information focuses on California quail. Currently the state-wide surveys for quail are limited to the North American Breeding Bird Survey (BBS) and the Audubon Christmas Bird Count. We used BBS data (1970–2013) to create abundance maps for quail throughout California. We developed 5-year averages to account for boom-and-bust cycles, and then established 100 random points for mountain and California quail, and 60 random points for Gambel's quail. Mountain quail populations have declined from high counts in the late 1970s. California quail populations peaked in the early 1990s, declined in the early 2000s, rebounded and are currently declining again. Gambel's quail populations peaked in the mid-1990s and in 2004, but have been declining since. Currently we are comparing quail population trends to road density, human population, and land use on a broad-scale. Improving our understanding of California's quail species requires research and monitoring across multiple spatial scales at which their population dynamics are influenced. At the large-scale (statewide), we are developing fall quail surveys to monitor population trends. Additionally, we are continuing fine-scale (local) counts at water sources and other locations. There is a poor understanding of western quail biology relative to northern bobwhite, therefore our new management plan will focus on prioritized research needs, including the relationship of quail to habitat, home range estimation, methods for population estimation that include detection probabilities, and genetic diversity and population structure.

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Key words: Breeding Bird Survey, *Callipepla californica*, *Callipepla gambelii*, management plan, *Oreortyx pictus*

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RANGES AND MOVEMENTS OF MONTEZUMA QUAIL IN SOUTHEAST ARIZONA

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ABSTRACT

Historical assumptions about Montezuma quail movements and home ranges at the population level are limited due to the lack of mark-recapture studies on this species from which solid conclusions can be derived. Such information is crucial for estimating population sizes, densities, and rate of emigration and immigration throughout the landscape. Our study examined home range size of 29 Montezuma quail and movements of 65 quail in southeast Arizona from 2008–2010. We used radio telemetry to follow radio-tagged birds in 3 study sites that varied in vegetation composition and topography. Mean home range size (MCP) was about was similar (51 ha) to the largest use area (50 ha) described in the literature for this species. The largest MCP home range estimate (206.7 ha) was far larger than what has been reported in the literature. Within a season, the largest mean maximum distance moved between 2 locations was 1,128.4 ± 619.5 m and the largest maximum linear distance between 2 locations for an individual was 2,375.5 m. Results from our research should help to address knowledge gaps about Montezuma quail home ranges and movements and provide a baseline to assist management of this species in the future.

Citation: Chavarria, P. M., N. J. Silvy, R. R. Lopez, D. S. Davis, and A. Montoya. 2017. Ranges and movements of Montezuma quail in Southeast Arizona. National Quail Symposium Proceedings 8:359–368.

Key words: *Cyrtonix montezumae, home* range, Mearn's quail, Montezuma quail, movements,

Understanding the home ranges and movements of wildlife populations is integral to their conservation. Ecological knowledge about the spatial-temporal dynamics associated with a species' life history, site use, and habitat requirements is especially important for management of game species in North America. Of North American gamebirds, much is known about northern bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*), but few studies in the literature have evaluated the movements and home range of Montezuma quail (*Cyrtonyx montezumae mearnsi*). Knowledge gaps associated for this species have been in large part due to the difficulty of locating and monitoring wild populations of these secretive birds as well as a lack of more efficient and effective methods for their capture in mark-and-release studies. Much of what is known about Montezuma quail ranges in the literature is asserted from anecdotal evidence and casual field observations of wild populations.

Claims about abundances and population densities in a local area can be derived with some certainty through the dog-assisted flush-count method, but any other conclusions about covey home ranges lack considerable accuracy if those populations are not monitored through a mark-recapture method—of which radio-telemetry provides one such means. Of the few radiotelemetry studies attempted for this species, only Stromberg (1990) was successful in estimating, to some extent, the home range size of this species. Stromberg's (1990) limited sample size, however, reduces the power from which conclusions can be derived and hypotheses tested regarding this species' movements and home ranges throughout the landscape. A need exists, therefore, to address this knowledge gap to resolve management and conservation

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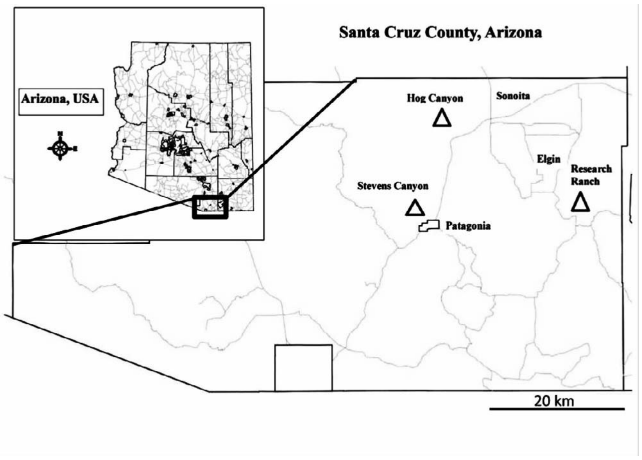

Fig. 1. Map of Montezuma quail study sites in Santa Cruz County, Arizona, 2007– 2010.

objectives for this species' distribution across the southeast Arizona region. Our goal in this study was to improve upon previous attempts at monitoring this species through radiotelemetry and to evaluate movements and seasonal ranges of Montezuma quail (Chavarria 2013). Our objectives were to verify the validity about previous conclusions made about this species' ranges and from comparison to our findings, provide meaningful conclusions, which could serve to facilitate the conservation and management of this species in the future.

METHODS

Study Site Selection

We conducted our study from 1 January 2008–31 May 2010 at 3 sites in southeast Arizona (Fig. 1), separated by 12.2 to 25.8 km from one another, to evaluate ranges and movements of spatially independent (quail did not move between sites) subpopulations across the landscape (Chavarria 2013). Diversity of habitat variables, particularly major vegetation types and topography, and how these could potentially affect home ranges and movements, were accounted for in study site selection. Of these sites, two were located in public lands managed by the Coronado National Forest (CNF). Steven's Canyon located along State Route 82 in Patagonia, Santa Cruz County and Hog Canyon along State Route 82, located closer to Sonoita, Santa Cruz County, were both within CNF boundaries. Hunting of Montezuma quail was permissible at both Steven's Canyon and Hog Canyon under legal Arizona Game and Fish (AZGF) permit, so those served as experimental treatments for evaluating potential impacts of hunting on their home ranges and their movements. The third site was at the Appleton-Whittell Research Ranch (AWRR) in Elgin, Santa Cruz County. AWRR was private land managed with an emphasis on research on native grassland communities in southeast Arizona. It was jointly managed by the National Audubon Society and Bureau of Land Management. AWRR was considered a "sanctuary" and, as such, did not permit legalized hunting. It served as a control site for evaluating home ranges and movements independent of impacts associated to hunting, grazing, and other sources of anthropogenic pressures realized in public lands across southeast Arizona.

Madrean Evergreen Woodland and Montane Meadow dominated Hog Canyon for vegetation and Caralampi gravelly sandy loam (22.2%) soils (Natural Resources Conservation Service [NRCS] 2012). Steven's Canyon also was dominated (52.8%) by Caralampi gravelly sandy loam soils (NRCS 2012) and had similar vegetative characteristics to Hog Canyon, but with a reduced over story canopy layer; Madrean Evergreen Woodland was sparser and intermixed with Desert Scrub mid story species (i.e., *Acacia* sp.; mesquite, *Prosopis* sp.). The AWRR consisted mainly of Plains and Great Basin Grasslands dominated by big sacaton (*Sporobolus wrightii*) bottomlands along Turkey Creek and Madrean Evergreen Woodlands sparsely dispersed among the sloping hills (Stromberg 1990), but were generally found in greater abundance and densities along the southern and eastern borders that neighbor the Coronado

National Forest (CNF). Dominant soils (52.5%) at AWRR consist of White House gravelly loam (NRCS 2012). Grazing of cattle was permitted seasonally at Hog Canyon and Stevens Canyon and was administrated by the CNF. Climate data from the nearest long-term weather station (Canelo, Arizona) indicated mean temperatures of 22.6^0 C in June, the hottest month, and mean temperature of 6.3^0 C in January, the coldest month, from 1981to 2010 for this region (Western Regional Climate Center 2012).

Capture and Handling

We captured quail from 1 January to 31 May 2008 in Stevens Canyon, from 6 December 2008 to 31 May 2009 in Hog Canyon, and from 12 February 2009 to 11 March 2010 on AWRR. The primary means of capturing Montezuma quail was by using large hoop-nets (Brown 1976) or throw-nets at night, when Montezuma quail were on their roosts. This required assistance of trained dogs, which would located birds by scent and hold point until the quail were cautiously approached and captured by researchers (Chavarria et al. 2012). A lightweight and transportable FLIR (Forward Looking Infra-Red) camera (FLIR Systems, North Billerica, Massachusetts) was sometimes used to narrow-down the location of quail by tracking their heat signatures after a dog had gone on point (Chavarria et al. 2012). Wire-cage funnel traps, baited with scratch seed, also were used with limited success. Other adaptations of audio (i.e., recorded callbacks) and visual lures (i.e., taxidermy mounts) also were sometimes used in conjunction with these funnel traps.

Captured birds were placed into individual cloth sacks, transported in a small, mobile field holding pen at the trap location, and later fitted with numbered aluminum leg bands and a mortality-sensitive, backpack radio-transmitter (about 5–9 g, less than 5% of bodyweight; 150.000-151.000 MHz; Wildlife Materials, Murphysboro, Illinois, USA; Telemetry Solutions, Concord, California, USA). We recorded gender and age for each individual. We determined approximate age of birds by examining fully developed presence of adult plumage on the facial feathers as well as the primary coverts using methods developed by previous researchers (Leopold and McCabe 1957, Stromberg 1990). Adult birds also were referenced as After-Hatch- Year (AHY) and juveniles and sub-adults were referenced as Hatch-Year (HY).

Most birds caught in night-trapping sessions were held overnight in a holding pen at the research station in Patagonia, Arizona or at the Appleton-Whittell Research Ranch and released before daybreak the following morning. Birds ($n = 5$) that were injured during the course of trapping were kept for 1–2 days in a holding pen at the research station and allowed time to recuperate and then relocated near their original covey. If a bird was non-releasable due to serious injury ($n = 2$) after 1–2 days, they were taken to a wildlife rehabilitation center (Liberty Wildlife Rehabilitation, Prescott, Arizona, USA) and treated for injuries. If treatment at the rehabilitation center was successful, birds ($n = 1$) were radio-tagged once again and released back into the wild near their original covey. If not ($n = 1$), the wildlife rehabilitation center became responsible for the care and oversight of non-releasable birds.

Radiotelemetry

We intended to fit at least 16 transmitters stratified by age class (i.e., juvenile or adult) and gender, among 3–4 coveys at each study site. This would allow for comparisons of home ranges and movements within these different classes and provide a moderate sample size for statistical evaluation. A 3-element Yagi antenna and ATS receiver (Advanced Telemetry Systems, Isanti, Minnesota, USA) were used to track individuals by vehicle from roads and off-road by foot.

Radio-tagged individuals, and the coveys with which they associated, were generally monitored at least 3–5 times a week at random times stratified by day (0700–1900 hours), when quail were most active, or night (1901–0659 hours), when quail were primarily on their roosts. An exception to this was the 2010 season where only the AWRR site were each quail was relocated each day at a random stratified times. All data collected, including quail sightings and quail sign (i.e., tracks, nesting sites, roosts, foraging sites), was entered into a database. Exact times and locations of visually relocated birds were georeferenced with a Garmin Legend GPS unit using Universal Transverse Mercator (UTM) coordinates in the NAD83 datum. Software programs ArcView 3.2a GIS (ESRI 2000) and QGIS (Quantum GIS Development Team 2011) were used to produce maps of location data using available 1:24,000 topographic maps [7.5-minute quadrangle, United States Geological Survey (USGS), Denver, Colorado, USA] and other available GIS layers.

Triangulation of radio-tagged individuals was conducted 3–5 times per week to estimate the locations of birds when they could not be visually relocated. Flush relocations and visual re- sightings were conducted 1–2 times per month prior to the breeding and nesting season to determine covey sizes and potential nest sites. Triangulation was conducted more often than flushing and walks-ins to reduce impact of field tracking as a possible means of disturbing movements of radio-tagged individuals and their coveys. At least 3 location bearings, but generally 4–5, spaced apart about 5 minutes in interval between subsequent observations, were used to derive estimates of a position during triangulation. When fewer ($n < 4$) locations were taken, we optimized bearing angles, where possible, to be 120 degrees from one another to reduce error estimating a location (Saltz 1994). The Maximum Likelihood Estimator (MLE; Lenth 1981) function in software LOAS 4.0.3.7 (2010) was used to estimate locations of individuals for which triangulated positions were collected. The MLE function was set to estimate a location with an accuracy of 1.0×10^{-6}, using a total of 60 iterations. Where few bearings were provided and accurate estimates could not be derived with the MLE, we set program LOAS to automatically derive location estimates using the Harmonic Mean (HM) or Best Biangulation (BB) functions. The HM function is "far less sensitive to outliers than either the arithmetic mean or the geometric mean, but it is still a variation of the classical method of determining location of a signal" (LOAS 2000). The BB function is used automatically by LOAS when there are only two bearings available (LOAS 2000).

Home Range Analysis

Montezuma quail home ranges were estimated using both the fixed kernel range (Worton 1989) estimator and the minimum convex polygon (MCP) method (Jennrich and Turner 1969) function provided by the Home Range Extension (Rodgers and Carr 1998) in ArcView 3.2a (Environmental Systems Research Institute 2000). We determined the number of locations needed (18 locations) to describe a home range by graphing home range area by number of relocations. However, for Stevens Canyon in 2008, we used a minimum of seven locations to determine home range size. This was done to compare MCP home ranges as determined by Stromberg (1990) who had a maximum of seven (range 4–7) relocations during his study. We used both MCP and fixed kernel methods to be able to compare with previous Montezuma quail MCP ranges (i.e., Stromberg 1990) and to provide fixed kernel range data for future studies on Montezuma quail. For the MCP method, we used 100% of the points to estimate the area (ha) used. Using the fixed kernel range method, we estimated the total range (ha) utilized (95% probability area, FK95) and core areas (50% and 25% probability areas, FK50 and FK25) for each individual. The fixed kernel estimator allows evaluation of utilization distributions (UD) rather than just simple home range outlines (Kernohan et al. 2001) such as those produced by the minimum convex polygon method (Jennrich and Turner 1969). It has advantages over the adaptive kernel method in that it is less likely to overestimate a home range area (Powell 2000) and it is generally supported as the best method currently available (Seaman and Powell 1996;

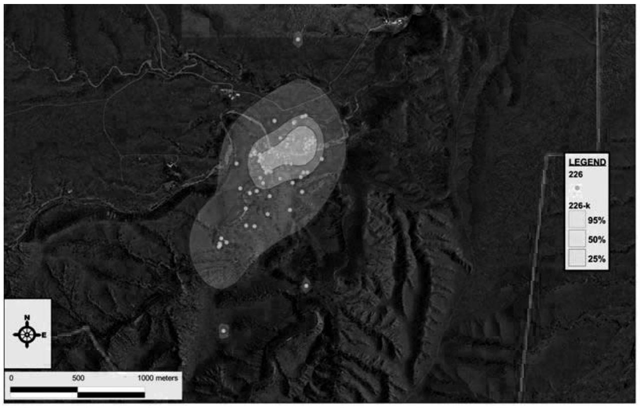

Fig. 2. Montezuma quail home range for HY female #226 showing 25%, 50%, and 95% Kernel utilization distributions at the Appleton-Whittell Research Ranch 2009.

Powell 2000; Kernohan et al. 2001). Home ranges (ha) and core areas (ha) were calculated for each individual and evaluated by study site, sex, age-class and season. Seasons were defined by the years in which field research was conducted at each individual site; these were generally from January–August each year, with some individuals surviving through December. Ranges for all radio-marked individuals, using FK25, FK50, and FK95 UD distributions, as seen in an example (Fig. 2), were plotted in ArcView 3.2a and QGIS.

Utilization distributions were derived using software JMP (SAS Institute Inc. 2007) and include mean hectares, range of hectares, mean days tracked, range of days tracked, mean number of locations, and range of number of locations for all individuals, as well as for the different age and sex classes, for each study site. The Adehabitat analysis package (Calenge 2006) for software R (R Development Core Team 2005) was used to evaluate other seasonal movement statistics including the following: mean maximum distance moved, maximum linear distance moved by an individual, the grand mean of distance moved between observations for all individuals, and the mean distance moved between first and last observation for all individuals.

RESULTS

Montezuma Quail Home Ranges

Stevens Canyon.—Home ranges and utilization distributions were evaluated for Stevens Canyon only for the 2008 field season (Tables 1 and 2). We tracked 10 individuals for a mean

31.1 ± 19.0 days, and mean 5.4 ± 2.3 for number of locations (Table 1Home ranges using the MCP method produced small mean home range size (24.6 ± 22.9 ha) for all quail at this site with the average MCP home range size being larger for males than females (Table 2). The mean FK50 UD (28.7 ± 20.9) for all quail was similar to

Table 1. Demographics of radio-marked Montezuma quail radio tracked in southeastern Arizona, 2008–2010. Ages: AHY = After-hatch-year (Adult), HY = Hatch-year (Juvenile).

Study area	Sex	Age	N	Locations (mean ± *SD*)	Locations range	Days (mean ± *SD*)	Days range
Stevens Canyon 2008	Male	AHY	4	5.3 ± 3.3	3–10	34.0 ± 23.3	6–60
		HY	0	-	-	-	-
	Female	AHY	5	5.4 ± 1.8	3–7	30.8 ± 19.3	16–60
		HY	1	6	6	21	21
	Total		10	5.4 ± 2.3	3–10	31.1 ± 19.0	6–60
Hog Canyon 2009	Male	AHY	1	5	5	34	34
		HY	7	23.9 ± 26.0	3–69	61.1 ± 49.9	7–145
	Female	AHY	1	53	53	97	97
		HY	3	27.3 ± 32.3	3–64	74.7 ± 61.3	10–132
	Total		12	25.6 ± 25.8	3–69	65.3 ± 47.5	7–145
Appleton- Whittell Research Ranch 2009	Male	AHY	4	22.8 ± 23.0	8–57	60.0 ± 61.2	13–150
		HY	8	29.9 ± 23.6	6–63	57.6 ± 39.7	8–112
	Female	AHY	4	36.3 ± 17.9	14–57	112.0 ± 52.2	70–185
		HY	8	34.1 ± 31.6	4–92	78.9 ± 72.8	8–211
	Total		24	31.2 ± 24.6	4–92	74.2 ± 57.7	8–211
2010	Male	AHY	3	7.3 ± 2.1	5–9	9.0 ± 5.0	4–14
		HY	7	10.4 ± 5.7	7–22	10.4 ± 3.7	7–18
	Female	AHY	5	17.0 ± 10.9	10–36	20.0 ± 13.8	11–44
		HY	4	14.0 ± 4.9	10–21	13.8 ± 3.6	11–19
	Total		19	12.4 ± 7.3	5–36	13.4 ± 8.4	4–44
All sites combined	Male	AHY	12	11.6 ± 14.7	3–57	34.0 ± 23.3	6–150
		HY	22	21.8 ± 21.4	3–69	43.7 ± 42.2	4–145
	Female	AHY	15	20.9 ± 18.3	10–57	53.3 ± 49.4	11–185
		HY	16	26.0 ± 23.0	3–92	58.2 ± 62.3	8–211
	Total		65	20.7 ± 21.2	3–92	48.2 ± 48.7	4–211

Table 2. Home ranges (ha; 100% minimum convex polygon [MCP], 50% fixed kernel distribution [FK50], and 95% fixed kernel distribution [FK95]) for radio-marked Montezuma quail in southeastern Arizona, 2008–2010. Ages: AHY = After-hatch-year (Adult), HY = Hatch-year (Juvenile).

				MCP		FK50		FK95	
Study area	Sex	Age	N	Mean ± *SD*	Range	Mean ± *SD*	Range	Mean ± *SD*	Range
Stevens Canyon[a] 2008	Male	AHY	1	49.3	49.3	15.7	15.7	183.6	183.5
		HY	0	-	-	-	-	-	-
	Female	AHY	2	12.2 ± 11.6	4.0–20.4	19.7 ± 19.6	5.8–33.5	95.5 ± 100.6	24.3–166.6
		HY	0	-	-	-	-	-	-
	Total	All	3	24.6 ± 22.9	4.0–49.3	28.7 ± 20.9	5.8–46.7	124.8 ± 87.5	24.3–183.6
Hog Canyon 2009	Male	AHY	0	-	-	-	-	-	-
		HY	3	46.3 ± 37.2	11.3–97.7	3.7 ± 2.2	1.5–5.8	71.0 ± 48.1	22.0–136.4
	Female	AHY	1	24.4	24.4	6.5	6.5	37.0	37.0
		HY	2	94.1 ± 48.8	45.3–142.9	9.4 ± 1.2	8.5–10.3	136.5 ± 5.6	131.0–136.5
	Total	All	6	58.6 ± 51.1	11.3–142.9	6.1 ± 3.1	1.5–10.3	87.2 ± 55.1	22.0–126.5
Appleton-Whittell Research Ranch 2009	Male	AHY	2	106.5 ±141.7	6.3–206.7	28.1 ± 33.6	4.4–51.9	153.6 ± 188.6	20.3–287.0
		HY	5	54.1 ± 41.9	11.7–98.3	27.3 ± 21.1	7.5–52.5	117.8 ± 90.1	32.4–219.2
	Female	AHY	3	41.8 ± 15.1	25.5–55.3	13.5 ± 14.5	5.0–30.3	66.3 ± 42.2	32.4–115.3
		HY	6	52.6 ± 56.1	5.6–150.2	33.0 ± 22.6	5.4–62.4	84.0 ± 131.0	19.1–228.9
	Total	All	16	64.2 ± 56.8	5.6–206.7	27.4 ± 20.7	5.0 ± 62.4	118.9 ± 88.3	19.1–287
2010	Male	AHY	0	-	-	-	-	-	-
		HY	1	19.0	19.0	5.1	5.1	33.1	33.1
	Female	AHY	2	6.2 ± 0.4	5.9–6.5	2.7 ± 0.2	2.6–2.9	14.4 ± 1.3	14.4–15.3
		HY	1	3.3	3.3	1.8	1.8	7.6	7.6
	Total	All	4	8.6 ± 7.0	3.3–19.0	3.1 ± 1.4	1.8–5.0	17.4 ± 11.0	7.6–33.1
All sites combined	Male	AHY	3	87.4 ± 105.5	6.3–206.7	24.0 ± 24.8	4.4–51.9	163.6 ± 134.5	20.0–287.0
		HY	9	47.6 ± 36.8	11.3–98.3	17.0 ± 19.3	1.5–52.5	92.8 ± 75.2	22.0–219.2
	Female	AHY	8	23.3 ± 18.7	4.0–55.3	13.7 ± 13.2	2.6–30.3	57.0 ± 54.7	14.4–166.6
		HY	9	56.3 ± 54.6	3.3–150.2	24.5 ± 22.1	1.8–62.4	87.2 ± 110.2	7.6–228.9
	Total	All	29	51.3 ± 51.8	3.3–206.7	19.8 ± 19.6	1.5–62.4	99.0 ±81.0	7.6–287.0

[a] For Stevens Canyon (2008), we used a minimum of 7 radio-telemetry locations to determine home ranges, but in all other study areas we use a minimum of 18 radio-telemetry locations to determine home ranges.

that of the MCP for all quail, but was the mean FK95 UD (125.8 ± 87.6) for all quail at this site were about 5.1 times larger than the mean MCP for this site (Table 2). The largest estimated home range for an individual using the MCP method was 49.3 ha and 183.6 ha using the FK95 UD method. Home ranges also were evaluated for different gender and age classes at Stevens Canyon (Table 2). Using the MCP method, the AHY male a larger home range size (49.3 ha) than the mean home range sizes (12.2 ha) for the two AHY females (Table 1). When using the fixed kernel method, both the FK50 and FK95 UDs ranges were larger for the male than the two females (Table 2). A comparison in mean home range size could not be made between HY females and HY males because no HY males were captured and marked and not enough location were obtained for HY females to calculate a home range.

Hog Canyon.—Home ranges and utilization distributions were evaluated for Hog Canyon only for the 2009 field season (Tables 1 and 2). We tracked 12 individuals for a mean of 65.3 ± 47.5 days and a mean 25.6 ± 25.8 for number of locations (Table 1). Home ranges using the MCP method produced moderate home range size (58.6 ± 51.1 ha) for the 6 quail with 18 or more locations at this site. The average MCP home range size was larger for HY females (94.1 ± 48.8 ha) than HY males (46.3 ± 37.2 ha) and both larger than the home range (24.4 ha) of the AHY female (Table 2). The FK50 and FK95 means were 9.6 times smaller and 1.5 times larger, respectively, than mean MCP ranges for quail at this site (Table 2). The largest estimated home range for an individual using the MCP method was 142.9 ha and 136.5 ha using the FK95 UD method. With the FK50 method, females of all age classes had substantially larger mean home range sizes when compared to HY males (Table 2).

Research Ranch: 2009.—Home ranges and utilization distributions were evaluated separately for the AWRR for the 2009 season (Tables 1 and 2). We tracked 24 individuals for a mean of 74.2 ± 57.7 days and a mean 31.2 ± 24.6 for number of locations (Table 1). Home ranges using the MCP method produced a moderate home range size (64.2 ± 56.8 ha) for quail with 18 or more locations at this site with the average MCP home range size being larger for AHY males (106.5 ± 141.7) than AHY females (41.1 ± 15.1; Table 2). The FK50 means were lower for all age and gender classes when compared to MCP (Table 2). FK95 means were larger within all age classes when compared to MCP. The largest estimated home range for an individual using the MCP method was 206.7 ha and 287.0 ha when using the FK95 UD method.

Table 3. Movement distances (meters ± *SD*) between successive observations for radio-marked Montezuma quail in southeast Arizona, 2008–2009. AHY = after hatch year (adult), HY= hatch year (juvenile). Statistics include number (N) of individuals, number of locations (mean ± *SD*, range), maximum distance moved, maximum linear distance, average distance moved between observations (mean ± *SD*), and distance between first and last observation (mean ± *SD*).

	Study site				
	Stevens Canyon	Hog Canyon	Appleton-Whittell Research Ranch		
Year	2008	2009	2009	2010	All Sites
N Individuals	10	12	24	19	65
N Locations (mean, range)	5.4 (3–10)	25.6 (3–69)	31.2 (4–92)	12.4 (5–36)	20.7 (3–92)
Maximum distance moved (mean)	678.4 ± 485.5	1,068.9 ± 741.2	1,128.4 ± 619.5	445.0 ± 179.3	848.5 ± 604.9
Maximum linear distance (individual)	1,339.6	2,375.5	2,250.4	894.8	2,375.5
Average distance moved between observations (mean)	302.8 ± 189.1	278.8 ± 106.0	239.2 ± 246.8	156.0 ± 61.8	232.0 ± 181.3
Distance between first and last observation (mean)	387.9 ± 297.5	373.3 ± 226.5	676.8 ± 533.7	227.4 ± 131.8	445.0 ± 405.2

Home ranges were evaluated for different gender and age classes (Table 2) with mean home range size for HY age classes (54.1 ± 41.9 ha and 52.6 ± 56.1 ha for males and females, respectively) were similar to AHY female ranges (41.8 ±15.1 ha), but about half the size of mean AHY male mean home range size (106.5 ± 141.7 ha; Table 2). In the FK50 estimates mean ranges were similar within all but AHY females which had a smaller mean home range size that all other. FK95 home range estimates had males with larger mean ranges sizes than females (Table 2).

Research Ranch: 2010.—Home ranges and utilization distributions were evaluated separately for the AWRR for the 2010 season (Tables 1 and 2). Nineteen individuals were tracked for a mean 13.4 ± 8.4 days and a mean 12.4 ± 7.3 for number of locations (Table 1). Home ranges using the MCP method produced small home range sizes (8.6 ± 7.0 ha) for the 4l quail at this site for which we had at least 18 locations, with a HY male having a larger home range size (19.0 ha) than the 2 AHY females (6.2 ± 0.4 ha) and the HY female (3.3 ha; Table 2). The FK50 means were smaller than those derived using the MCP method for all age and gender classes (Table 2). However, the FK95 mean home range estimates were larger when compared to MCP mean home range size (Table 2). The largest estimated home range for an individual using the MCP method was 19.0 ha and 33.1 ha using the FK95 UD method.

All Sites Combined: 2008–2010.—Home ranges and utilization distributions were evaluated for all site combined (Tables 1 and 2). We tracked 65 individuals for a mean of 48.2 ± 48.7 days and a mean 20.7 ± 22.2 for number of locations (Table 1). Home ranges using the MCP method produced a mean home range size (51.3 ± 51.8 ha) for 29 quail on the three study sites. The average MCP home range size was larger for AHY males (87.4 ± 105.5 ha) than HY males (47.6 ± 36.8 ha), AHY females (23.3 ± 18.5 ha), and HY females (56.3 ± 54.6 ha; Table 2). The FK50 and FK95 means were 2.6 times smaller and 1.9 times larger, respectively, than mean MCP ranges for quail at this site (Table 2).

Montezuma Quail Movements

Stevens Canyon.—Movement distances were calculated for 10 individual quail at Stevens Canyon for the 2008 season (Table 3). The mean maximum distance moved by all quail at this site was 678.4 ± 485.5 m. The maximum linear distance between two locations within the home range of an individual at this site was 1,339.6 m. The grand mean for average distance moved between successive observations for all birds at this site was 302.8 ± 189.1 m. Lastly, the mean distance between first and last observation was 387.9 ± 297.5 m. Movement statistics also were evaluated by gender and age class for the 2008 season (Table 4). The mean maximum distance moved was larger for females (AHY = 771.3 ± 519.1 m and HY = 867.6 m) than males (AHY = 515 ± 534.8 m), and the HY female had the largest mean. Both

Table 4. Movement distances (meters ± *SD*) by age class and gender between successive observations for radio-marked Montezuma quail at Stevens Canyon, southeast Arizona, 2008. AHY = after hatch year (adult), HY= hatch year (juvenile). Statistics include number (N) of individuals, number of locations (mean ± *SD*, range), maximum distance moved, maximum linear distance, average distance moved between observations (mean ± *SD*), and distance between first and last observation (mean ± *SD*).

Age Class	AHY Female	HY Female	AHY Male	HY Male	All quail
N Individuals	5	1	4	0	10
N Locations (mean, range)	5.4 (3–7)	6 (6)	5.3 (3–10)	-	5.4 (3–10)
Maximum distance moved (mean)	771.3 ± 519.1	867.6	515.1 ± 534.8	-	678.5 ± 485.5
Maximum linear distance (individual)	1,339.6	867.6	1,316.4	-	1,339.6
Average distance moved between observations (mean)	328.7 ± 196.8	305.2	269.8 ± 230.4	-	302.8 ± 189.1
Distance between first and last observation (mean)	388.8 ± 357.8	640.6	323.6 ± 260.7	-	387.9 ± 297.5

Table 5. Movement distances (meters ± *SD*) by age class and gender between successive observations for radio-marked Montezuma quail at Hog Canyon, southeast Arizona, 2009. AHY = after hatch year (adult), HY= hatch year (juvenile). Statistics include number (N) of individuals, number of locations (mean ± *SD*, range), maximum distance moved, maximum linear distance, average distance moved between observations (mean ± *SD*), and distance between first and last observation (mean ± *SD*).

Age Class	AHY Female	HY Female	AHY Male	HY Male	All Quail
N Individuals	1	3	1	7	12
N Locations (mean, range)	53 (53)	27.3 (3–64)	5 (5)	23.86 (3–69)	25.2 (3–69)
Maximum distance moved (mean)	754.3	1,531.4 ± 908.1	312.9	1,023.6 ± 714.9	1,068.9 ± 741.2
Maximum linear distance (individual)	754.3	2,375.5	312.9	2043.9	2043.9
Average distance moved between observations (mean)	163.8	377.9 ± 69.9	140.0	272.5 ± 92.8	278.8 ± 106.0
Distance between first and last observation (mean)	268.7	362.4 ± 22.0	259.8	409.2 ± 297.3	373.3 ± 226.5

the AHY females (1,339.6 m) and AHY males (1,316.4 m) had similar maximum linear distance moved, but this was lower for the only HY female (867.6 m) observed (Table 4). The average distance moved between observations was similar between AHY females (328.7 ± 196.8 m) and AHY males (269.8 ± 230.4 m; Table 4). No HY males were monitored so those movement data are unavailable for that age-gender class.

Hog Canyon.—Movement distances were calculated for 12 individuals at Hog Canyon for the 2009 season (Table 3). The mean maximum distance moved by quail at this site was 1,068.9 ± 741.2 m (Table 3). The maximum linear distance between two locations within the home range of an individual at this site was 2,375.5 m. The grand mean for average distance moved between successive observations for all birds at this site was 278.8 ± 106.0 m. Lastly, the mean distance moved between first and last observation was 373.3 ± 226.5 m. Movement data also were evaluated by gender and age class for the 2009 season (Table 5). The mean maximum distance moved was larger for HY males (1,023 ± 714.9 m) and HY females (1,531.5 ± 908.1 m) than for AHY males (312.9 m) and AHY females (754.3 m; Table 5). Maximum linear distance moved also was considerably larger for HY males and females than AHY males and females, with the largest distance moved (2,375.5 m) pertaining to a HY female (Table 5). The average distance moved between observations also was larger for HY males and females than AHY males and females (Table 5).

Research Ranch: 2009.—Movement distances were calculated separately for the 2009 and 2010 seasons at the AWRR. Movements for 24 individuals were evaluated for the 2009 season (Table 3). In 2009, the mean maximum distance moved by all quail at this site was 1,128.4 ± 619.5 m. The maximum linear distance between two locations within the home range of an individual at this site was 2,250.4 m. The grand mean for average distance moved between successive observations for all quail at this site was 239.2 ± 246.8 m. Lastly, the mean distance moved between first and last observation was 676.8 ± 533.7. Gender and age class also evaluated movement distances for the 2009 season (Table 6). The mean maximum distance moved was larger for females than males when comparing within age classes (Table 6). Within gender, means were larger in AHY females (1,336.7 ± 217.7 m) than HY females (1,175.6± 841.7 m) and larger in HY males (1,070.2 ± 422.2 m) than AHY males (942.1 ± 840.9 m).

Maximum linear distance moved by an individual was larger in HY females (2,250.4 m), followed by AHY males (2,188.3 m). The average distance moved between observations also was larger in HY females (214.6 ± 22.1 m) and second largest in HY males (316.6 ± 420.2 m).

Research Ranch: 2010.—Movement statistics for 19 individuals were evaluated for the 2010 season (Table 3). In 2010, the mean maximum distance moved by all quail at this site was 445.0 ± 179.3 m. The maximum linear distance between two locations within the home range of an individual at this site was 894.8 m. The grand mean for

Table 6. Movement distances (meters ± *SD*) by age class and gender between successive observations for radio- marked Montezuma quail at the Research Ranch, southeast Arizona, 2009. AHY = after hatch year (adult), HY = hatch year (juvenile). Statistics include number (N) of individuals, number of locations (mean ± *SD*, range), maximum distance moved, maximum linear distance, average distance moved between observations (mean ± *SD*), and distance between first and last observation (mean ± *SD*).

Age Class	AHY Female	HY Female	AHY Male	HY Male	All Quail
N Individuals	4	8	4	8	24
N Locations (mean, range)	36.3 (14–57)	34.1 (4–92)	22.8 (8–57)	29.9 (6–63)	31.2 (6–92)
Maximum distance moved (mean)	1,336.7 ± 216.7	1,175.6 ± 841.7	942.1 ± 840.9	1,070.2 ± 422.2	1,128.4 ± 619.5
Maximum linear distance (individual)	1,582.8	2,250.4	2,188.3	1,546.3	2,250.4
Average distance moved between observations (mean)	198.7 ± 22.1	214.6 ± 107.1	174.3 ± 48.6	316.5 ± 420.2	239.2 ± 246.8
Distance between first and last observation (mean)	535.8 ± 398.8	803.3 ± 702.0	510.3 ± 549.1	704.2 ± 446.7	676.9 ± 533.8

Table 7. Movement distances (meters ± *SD*) by age class and gender between successive observations for radio- marked Montezuma quail at the Research Ranch, southeast Arizona, 2010. AHY = after hatch year (adult), HY = hatch year (juvenile). Statistics include number (N) of individuals, number of locations (mean ± *SD*, range), maximum distance moved, maximum linear distance, average distance moved between observations (mean ± *SD*), and distance between first and last observation (mean ± *SD*).

Age Class	AHY Female	HY Female	AHY Male	HY Male	All Quail
N Individuals	5	4	3	7	19
N Locations (mean, range)	17 (10–36)	14 (10–21)	7.3 (5–9)	10.4 (7–22)	12.4 (5-36)
Maximum distance moved (mean)	425.5 ± 109.4	487.1 ± 228.5	450.8 ± 98.6	432.3 ± 239.6	445.0 ± 179.3
Maximum linear distance (individual)	486.1	758.1	542.6	894.8	894.8
Average distance moved between observations (mean)	135.7 ± 50.4	157.9 ± 47.5	230.7 ± 96.7	137.3 ± 44.5	156.0 ± 61.8
Distance between first and last observation (mean)	201.2 ± 123.6	278.1 ± 248.4	272.9 ± 26.7	197.7 ± 80.3	227.4 ± 131.7

average distance moved between successive observations for all birds at this site was 156.0 ± 61.8 m. Lastly, the mean distance moved between first and last observation was 227.4 ± 131.8 m. Movement statistics also were evaluated by gender and age class for the 2010 season (Table 7). The mean maximum distance moved was similar (range = 425.5 ± 109.4 m for AHY females to 487.1± 228.5 m for HY females) amongst all age and gender classes, but larger for HY females (Table 7). Maximum linear distance moved by an individual was larger for HY males (894.8 m) and second larger for HY females (758.1 m). The average distance moved between observations was similar for AHY females (135.7± 50.4 m), HY females (157.9± 47.5 m), and HY males (137.3± 44.5 m), but larger for AHY males (230, 7± 96.7 m).

All Sites Combined: 2008–2010.—Movement distances were calculated for 65 individuals for all sites combined (Table 3). The mean maximum distance moved by quail at all sites was 848.5 ± 604.7 m (Table 3). The maximum linear distance between two locations within the home range of an individual at this site was 2,375.5 m. The grand mean for average distance moved between successive observations for all birds was 232.0 ± 181.3 m. Lastly, the mean distance moved between first and last observation was 445.0 ± 405.2 m. Movement distances also were evaluated by gender and age class for all sites combined (Table 8). The mean maximum distance moved was larger for HY females (1,050.9 ± 769.7 m) than for HY males (852.4 ± 555.5 m), AHY males (624.5± 575.1 m) and AHY females (787.7± 474.6 m; Table 5). Maximum linear distance moved also was similar for HY males, AHY females and AHY males with the largest distance moved (2,375.5 m) pertaining to a HY female (Table 8). The average distance moved between observations was largest (245.5± 260.7 m) for HY males (Table 8).

DISCUSSION

Ranges ($n = 29$) and movement distances for 65 Montezuma quail were determined in southeast Arizona from 2008–2010. We encountered problems with radio-transmitter failure at the start of the 3-year study at Stevens Canyon, which limited the number of locations recorded for individual quail. At this site only we used a minimum of 7 locations to determine home range size, for without doing so we would not have been able to calculate home ranges for quail at this site. We justify doing so for this site because Stromberg (1990) used a maximum of seven locations to determine home range size during his study. For the other two sites, we used a minimum of 18 locations to determine home ranges. We calculated both MCP and fixed kernel home ranges for two reasons. First, we needed MCP home ranges data to compare to the only other study (Stromberg 1990) on home ranges for this species. In addition, we calculated 50% and 95% fixed kernel home ranges so as future researchers could use our results in their presentations.

For Hog Canyon and the AWRR, we were able to track some individuals for as long as 145 and 211 days,

Table 8. Movement distances (meters ± *SD*) by age class and gender between successive observations for radio- marked Montezuma quail for all sites combined, southeast Arizona, 2010. AHY = after hatch year (adult), HY = hatch year (juvenile). Statistics include number (N) of individuals, number of locations (mean ± *SD*, range), maximum distance moved, maximum linear distance, average distance moved between observations (mean ± *SD*), and distance between first and last observation (mean ± *SD*).

Age Class	AHY Female	HY Female	AHY Male	HY Male	All Quail
N Individuals	15	16	12	22	65
N Locations (mean, range)	20.7 (3–57)	26 (3–92)	7.3 (5–57)	10.4 (3–69)	12.4 (3–92)
Maximum distance moved (mean)	787.7 ± 474.6	1,050.9 ± 769.7	624.5 ± 575.1	852.4 ± 555.4	844.3 ± 605.5
Maximum linear distance (individual)	1,582.81	2,375.5	2,188.3	2,043.9	2,375.5
Average distance moved between observations (mean)	218.7 ± 137.9	236.7 ± 112.6	217.4 ± 138.2	245.5 ±260.7	232.0 ± 181.3
Distance between first and last observation (mean)	357.5 ± 306.2	579.2 ± 550.4	367.8 ± 335.4	449.2 ± 374.2	445.0 ± 405.2

respectively. These results surpass those found by Stromberg (1990) where the mean number of days captured birds were known to be alive was 28.4 days (*SE* = 8.9 days) and the longest time a radio-tagged bird was monitored was about 140 days.

We found Montezuma quail to be sedentary with small home range sizes. However, we documented wider variation by gender and age classes in the home range sizes and movements of Montezuma quail from our study sites. Stromberg's (1990) noted that coveys used small areas (0.09–6 ha) in the winter, non-overlapping areas as large as 50 ha in early spring and from June to October, pairs remained sedentary in small areas, often smaller than two ha. Coveys in his study were consistently relocated in the same small areas and usually within the same 50 m^2 area.

Home range estimates in our study spanned from late winter to late summer, with exception to the 2008 season at Stevens Canyon and 2010 season the AWRR where data were limited to only late winter and early spring. Mean seasonal home range size (MCP) for all sex and gender classes in our study averaged 51.3 ± 51.8 ha which was similar to largest use area (50 ha) derived by Stromberg (1990).

We did not track radio-tagged birds hourly or at 30-minute intervals, because we felt such intensive tracking could be intrusive and affect the behavior of birds being monitored.

Montezuma quail, especially those using open grasslands on arroyo bottoms, could often detect us from over 50 m and would flush into dense cover. Such aversive behavior has undesired impact on observing natural movements and determining accurate home ranges. Our method, therefore, allowed us to improve the accuracy of estimating home range areas with less worry that our monitoring activities artificially affecting estimates of their utilization distributions.

Large-scale migrations were not observed in our study and the mean distance between relocations, on sequential days, for all quail we observed, averaged 844.3± 605.5 m. Stromberg (1990) observed mean distance moved to be 97.8 m (*SE* = 15.1) from January to March, but increased to 194.9 m (*SE* = 56.8) for some birds from March to May. From July to October, Stromberg (1990) reported the mean distance moved between successive days to be 79.2 m (*SE* = 47.4).

Comparison between genders and different age classes, and the interaction of these, also revealed some important differences that occur in both home range size and movements. These differences need to be examined further in future studies with larger sample sizes of radio-marked birds that also account for diverse landscape features. In summary, home range size and movements varied by study site and may be explained by differences in features at the landscape and microhabitat level. Differences in range size between gender and age classes were observed between two study sites, but similarities within age classes were observed between the two sites. Our data corroborates historical assumptions about relatively small home range sizes for this species, but our estimates are much larger than those presented in the literature.

MANAGEMENT IMPLICATIONS

Understanding the home ranges and movements of wildlife populations is integral to their conservation. Our study of home range and movements of Montezuma quail on three study areas in southeast Arizona provided us an opportunity to add to the knowledge of this important species.

Based on our study, the following conclusions were drawn:

1. Montezuma quail are sedentary with small home range sizes.
2. Mean home range size for our three study areas was similar to that found in a previous study of the species.
3. Age and gender classes had similar ranges and movements.
4. Montezuma quail did not make large-scale migrations.
5. Montezuma quail in our study had much larger movements between sequential relocations than observed from a previous study.

Further research throughout the species is recommended to lend more support to conclusions drawn from our study in southeast Arizona. Such research is warranted for developing better management and conservation strategies for this species throughout its range.

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SURVIVAL DEMOGRAPHICS OF MONTEZUMA QUAIL IN SOUTHEAST ARIZONA

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ABSTRACT

Many facets of Montezuma quail (*Cyrtonyx montezumae mearnsi*) population dynamics, such as survival and causes of mortality, are unknown because of limited or lack of mark–recapture studies on wild populations of this species. Much of what is known about this species comes from casual observations in the field or from dog-assisted flush-count surveys. Further insight into rate and causes of mortality for this species is necessary to ensure proper conservation measures. We evaluated survival and causes of mortality of Montezuma quail in southeastern Arizona from winter 2007 to spring 2010. Survival was determined from quail captured, radiotagged, and monitored among 3 separate study sites. In 2 of these sites hunting was permitted; and in 1 site (the control) hunting was not permitted. Estimation of accurate mortality rates in hunted sites was complicated by large quantities of censored data, some of which was attributable to lack of reported mortalities from hunting. Mortality in the control site may have been compounded by a combination of stochastic events (i.e., wildfire, freezing) occurring during the study. Mortality rate for all sites were higher than any estimates reported or hypothesized in known scientific literature. The estimated rate of survival, combined among the 3 sites, was 21.9% from autumn 2008 to autumn 2009.

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Although past research has provided much insight into the natural history of the Montezuma quail (*Cyrtonyx montezumae mearnsi;* Wallmo 1954, Leopold and McCabe 1957, Bishop and Hungerford 1965), few studies have provided in-depth analysis of their population dynamics as derived from radiotelemetry analysis (Stromberg 1990). The few studies that have attempted monitoring of wild Montezuma quail populations through radiotelemetry have had complications associated with trapping a sufficient sample size, transmitter failure, negative impact of transmitters on radiomarked quail, or combinations of these effects (Stromberg 1990, Hernandez et al. 2009). Lack of successful mark–recapture and telemetry studies has contributed to gaps in knowledge about quail life history and poor estimates of their populations throughout their known range. A better understanding of the abundance, densities, and survival rate and causes of mortality in wild populations of the Montezuma quail is important for their conservation (Chavarria 2013); it is especially crucial in areas where they face selective pressures from anthropogenic sources such recreational hunting and grazing and are at additional risk from fire-affected habitats (i.e., prescribed burns, wildfires).

Our goal was to evaluate survival of Montezuma quail on 3 separate study sites in southeastern Arizona and determine causes of quail mortality. Our objectives were then to test whether differences occurred within and among study sites, treatments (hunting vs. nonhunting), sex, and age classes. Where possible, we examined

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differences in mortality rate among seasons as well as across the aforementioned strata. High rates of mortality are thought to occur within younger age classes of this species immediately following the hatch season (autumn–winter). This is mostly attributed to naïve behavior and undeveloped survival instincts by the younger age classes. High rates of mortality among adult age classes of this species are thought to occur during the breeding season, from May to August, because of risky behaviors associated with reproduction (i.e., courting displays and calls) or increased movements. Our objective was to evaluate survival and test for differences among study sites, sex, and age if data permitted.

STUDY AREAS

We conducted surveys of Montezuma quail throughout Arizona Game and Fish Department's Management Unit 35 in southeastern Arizona within areas administrated by the Coronado National Forest in Santa Cruz County. Most research was concentrated near Stevens Canyon and Smith Canyon in Patagonia; Apache Tank and Williamson Tank in the San Rafael Valley; Apache Spring, Hog Canyon, and Gardner Canyon near Sonoita; and Appleton–Whittell Research Ranch (AWRR) near Elgin (Chavarria 2013). Trapping and long-term monitoring of radiomarked individuals occurred primarily in Stevens Canyon, Hog Canyon, and AWRR.

METHODS

Capture and Handling

Man-hours and dog-hours invested in trapping effort varied among study sites, but generally did not exceed 2–3 trap sessions/week, with sessions conducted ≥ 2 days apart, totaling no more than 15 man-and-dog hours/week (Chavarria et al. 2012a). We generally invested more trap-hours at the control site because potential conflicts with hunters at the experimental sites reduced opportunities for trapping during the hunting season (mid-Nov to early Feb).

We used a combination of techniques to capture Montezuma quail: wire-cage funnel traps, day trapping with hoop-nets and dogs, and night trapping with hoop-nets and dogs. Our primary means of trapping quail was initially to track birds with assistance of trained dogs, which held point until researchers cautiously approached and captured the quail with large hoop-nets (Brown 1976, Chavarria et al. 2012a) or throw-nets. At times we used a lightweight and transportable Forward Looking Infra-Red camera (FLIR Systems, North Billerica, MA, USA) to locate quail by tracking their heat signature at a location where a dog had gone "on point" (Chavarria et al. 2012a).

Upon capture, we placed birds into individual cloth sacks and then transported birds in a small and mobile field-holding pen at the trap location until we fitted them with a backpack radiotransmitter ($\sim$5–8 g, $<$5% of body mass; Wildlife Materials, Murphysboro, IL, USA) and evaluated them for morphological characteristics. We recorded gender, age, weight, wing length, tail length, head and bill length, culmen length, bill width, bill depth, and tarsus length for each individual bird. We determined age of birds from fully developed presence of adult plumage on the facial feathers as well as the primary coverts using methods developed by previous researchers (Leopold and McCabe 1957, Stromberg 1990). We referred to adult birds as After-Hatch-Year and juveniles and subadults as Hatch-Year. We fitted all captured birds with numbered aluminum leg bands. In the case of multiple captures or birds caught in night-trapping sessions, we held birds overnight in a holding pen at the research station in Patagonia, Arizona, or at the Appleton–Whittell Research Ranch and released them before daybreak the following morning. We did this to reduce possible mortality from hypothermia caused by releasing birds at night after covey displacement. We flight-tested radiotagged quail prior to releasing them to ensure that the attachment did not affect their ability to fly and thus did not reduce their chances of survival. Once ≥ 1 members of a covey were radiotagged, other members of the same covey could be trapped via Judas telemetry (Taylor and Katahira 1988). We recaptured many birds on >1 occasion so as to trap other members of their coveys in subsequent trapping sessions, or to replace transmitters with drained or fading batteries. We kept birds that were injured during trapping for 1–2 days in a holding pen at the research station and allowed them time to recuperate. If a bird was nonreleaseable after 1–2 days due to serious injury, we took it to a wildlife rehabilitation center (Liberty Wildlife Rehabilitation, Prescott, AZ, USA) and had it treated for injuries. If treatment at the rehabilitation center was successful, we radiotagged birds once again and released them back into the wild. If not, the wildlife rehabilitation center became responsible for the care and oversight of nonreleasable birds.

Radiotelemetry

We tracked radiotagged birds on a weekly basis. We monitored birds via triangulation of radio signal approximately 3–5 times/week at random times stratified by morning or afternoon. We conducted walk-ins and flush counts periodically on each radiotagged bird at least once every 3 weeks during the nonbreeding season. We did this to determine the health status of the radiotagged bird and size of the covey with which it was interacting, as well as to note habitat use, roost selection, nest-site selection, and other behavioral components (i.e., feeding, reproduction). We reduced frequency of walk-ins and flush counts during the breeding season to reduce potential impact to reproduction. We conducted night-time walk-ins at least once every 2 weeks during the breeding season to determine clutch size and hatch size if nests had been established. We took extra precautions not to flush birds during night-time walk-ins, especially during the breeding season so as to avoid disruption to breeding behavior and nesting.

Transmitters included built-in "mortality signals" to indicate long periods of inactivity or lack of movement, which alerted us that a marked bird was potentially

Table 1. Finite survival probability estimates (*S* ± SE) calculated using Kaplan–Meier staggered entry design (Pollock et al. 1989) for radiotagged Montezuma quail in southeastern Arizona for autumn 2008–2009 and winter 2009–spring 2010. Included in the table is sample size (*n*) for individuals trapped, and mean ± standard deviation (SD) and range for number of days tracked for each category.

Study site	*n*	Mean ± SD	Range	*S*	SE	Lower CI	Upper CI
Stevens							
All sexes	4	24.86 ± 18.91	5–60	0.750	0.217	0.326	1.00
Hog							
All sexes	13	61.77 ± 47.19	7–145	0.400	0.203	0.002	0.798
Ranch							
All sexes	31	62.13 ± 56.19	2–211	0.236	0.128	0.00	0.486
Subadult M	13	41.86 ± 39.39	2–112	0.238	0.191	0.00	0.612
Subadult Fs	9	71.4 ± 68.08	7–211	0.169	0.151	0.00	0.465
Adult M	4	60.0 ± 61.23	13–150	0.667	0.272	0.133	1.00
Adult F	5	112.0 ± 52.24	70–185	1.00	0.00	1.00	1.00
M (All)	17	83.0 ± 64.81	2–150	0.223	0.177	0.00	0.571
F (All)	14	45.89 ± 43.68	7–211	0.360	0.171	0.025	0.695
All sexes[a]	24	12.52 ± 8.47	2–44	0.048	0.037	0.00	0.120
All sites							
All sexes	50	42.53 ± 46.54	2–211	0.219	0.090	0.043	0.397

[a] Winter 2009–spring 2010. All other estimates represent autumn 2008–2009.

deceased or the transmitter was nearing battery failure. We investigated mortality signals and recovered carcasses if possible. We collected and preserved in a freezer any carcasses that remained mostly intact. We submitted some of these remains to Dr. Mark Stromberg at the collections facility at the University of California, Berkeley. We georeferenced locations of visually relocated birds using Universal Transverse Mercator coordinates, in the NAD83 datum, with a Garmin Legend (Garmin, Ltd., Olathe, KS, USA) Global Positioning System unit in ArcView. We also recorded aspects of their habitat use such as home range, vegetation selection, and topography.

Statistical Analysis

Survival.—We used the Kaplan–Meier staggered entry estimator (Pollock et al. 1989) to calculate survival rate (*S*) and distribution by treatment (hunting vs. nonhunting), sex, and age-class for tagged birds. We estimated annual survival rates from the beginning of one autumn season (starting 21 Sep) to the start of autumn season the following year. We determined seasonal survival rates for birds captured postautumn. We considered 4 seasons for analysis: 21 September–20 December (autumn), 21 December–20 March (winter), 21 March–20 June (spring), and 21 June–20 September (summer). We censored from analysis birds that survived from one autumn season to the next and readmitted them that following season. We also noted the total number of days during which we observed a bird during the study. We calculated survival rate and standard errors using the software program ECOLOGICAL METHODOLOGY (Krebs 2002). Where data allowed, we used the log-rank Chi-square test (Krebs 2002) to determine differences among annual or seasonal survival distributions by treatment (hunted vs. nonhunted), sex, and age-class, with significance value set at $P = 0.05$.

Mortality.—We categorized censored observations or losses from mortality into groups based on any available evidence at the recovery site: predation (avian, mammalian), hunted, unknown, and other (trap injury, trap stress, dropped transmitter).

RESULTS

Capture Success and Survival

We began trapping at the AWRR in February 2009 and captured 54 individual birds from 12 February 2009 to 11 March 2010: 7 adult males, 11 adult females, 21 juvenile males, and 15 juvenile females. We did not tag one other bird captured during this time because it died from dog-inflicted injury. In the 2009 season, we observed tagged individuals for an average of 62.13 ± 56.19 days (range = 2–211 days; Table 1). We observed a subadult male for the fewest days and a subadult female the most days. We confirmed 29 mortalities: 7 confirmed raptor kills (including 1 northern harrier [*Circus cyaneus*], 1 owl, and 1 Harris's hawk [*Parabuteo unicinctus*]), 1 confirmed mammal kill, 3 frozen on roost, 1 trap injury, and 17 mortalities with unknown cause. We censored 25 individual birds for reasons including fallen transmitters ($n = 3$), transmitter failures ($n = 9$), injury-rehabilitation ($n = 1$), untagged ($n = 1$), and unknown cause ($n = 11$). Finite survival probability of quail for autumn 2008–autumn 2009 was $S = 0.236 \pm 0.128$ for all sexes and age classes combined. Finite survival probabilities were all males only, $S = 0.223 \pm 0.177$; all females only, $S = 0.360 \pm 0.171$; adult males, $S = 0.667 \pm 0.272$; adult females, $S = 1.00 \pm 0.00$; juvenile males, $S = 0.238 \pm 0.191$; and juvenile females, $S = 0.169 \pm 0.151$. Finite survival probability for winter 2009–spring 2010 was $S = 0.048 \pm 0.037$ (Table 1). We did not calculate finite survival probabilities for separate sex and age classes for winter 2009–spring 2010. We tracked birds at the AWRR in 2010 for an average (±SD) of 12.52 ± 8.47 days (range = 2–44 days; Table 1).

We trapped 10 individual birds at Stevens Canyon from January to May 2008: 4 adult males, 1 juvenile male, 3 adult females, and 2 juvenile females. We did not calculate survival estimates for birds captured during that period because of transmitter problems and censored data. We captured 4 additional birds (1 ad M, 3 ad F) in autumn 2008 and monitored them successfully on a more consistent basis. We tracked these birds for an average (±SD) of 24.86 ± 18.91 days (range = 5–60 days; Table 1). We also captured, but did not tag, 3 other birds during this time (2 died from dog-inflicted injury and 1 died from stress during capture). We obtained a limited number of relocations for these birds, however, which led to us censoring them early in winter 2008–2009. Causes of censoring were confirmed hunting mortality ($n = 1$), and suspected hunting mortalities ($n = 3$).We received 1 radiotransmitter from a hunter with a letter describing the location, time, and date the bird had been shot. Finite survival probability estimated within this time interval was $S = 0.750 \pm 0.217$ (Table 1).

We began trapping at Hog Canyon in autumn 2008 and captured 13 individual birds from 6 December 2008 to 31 May 2009: 2 adult males, 1 adult female, 7 juvenile males, and 3 juvenile females. We tracked radiotagged individuals for an average (±SD) of 61.77 ± 47.19 days (range = 7–145 days; Table 1). We confirmed 4 mortalities (of which 2 were confirmed raptor kills), and we also censored 9 individuals. Some suspected hunting mortalities ($n = 2$) were later confirmed from reports submitted through AZGF wing barrel counts. Finite survival probability estimated within this time interval was $S = 0.400 \pm 0.203$. We calculated no survival probabilities within the different sex and age classes because of small sample size. We captured, but did not tag, 3 other birds during this time (2 died from dog-inflicted injury and 1 escaped capture before processing).

Finite rate of mortality for all sites combined for autumn 2008–autumn 2009 was $S = 0.219 \pm 0.090$. We tracked birds from all sites for an average of 42.53 ± 46.54 days (range = 2–211 days) throughout the study (Table 1). During the entire study at all study sites, we tracked females an average of 49.57 ± 53.79 days (range = 2–211 days) and males for an average of 36.47 ± 38.89 days (range = 2–150 days).

Hypothesis Testing

A large sample size and low censor ratio at the AWRR for the 2009 season allowed for log-rank Chi-square comparisons (Pollock et al. 1989) of weekly survival probabilities among different age–sex classes of radio-tagged Montezuma quail at that site. We analyzed survival probabilities for these groups where relocation histories overlapped within and between the different age–sex classes. We found no significant differences when comparing weekly survival probabilities between all males and all females ($\chi^2 = 0.01$, $P = 0.920$), between adult males and adult females ($\chi^2 = 0.33$, $P = 0.566$), between all juveniles and all adults ($\chi^2 = 0.141$, $P = 0.235$), between juvenile males and juvenile females ($\chi^2 = 0.030$, $P = 0.863$), or between adult males and juvenile males ($\chi^2 = 0.00$, $P = 1.00$). We found no significant difference in weekly survival probabilities between adult females and juvenile females ($\chi^2 = 0.277$, $P = 0.096$), but data showed a trend supporting higher survival probability for adult females.

DISCUSSION

From 2008 to 2010, we examined sources of mortality and survival demographics of Montezuma quail in-depth for the first time through the use of radiotelemetry. Existing literature on Montezuma quail provided information about probable sources of mortality from field observations but no actual mortality rates or survival estimates at the population or covey level (Leopold and McCabe 1957, Bishop 1964, Brown 1979). Stromberg's (1990) telemetry study provided the first estimates of survival and documented sources of mortality, but from a limited sample size ($n = 15$). Stromberg's tagged birds lived for an average of 28.4 days (SE = 8.9 days), with the longest time a tagged bird was observed before falling to predation being 140 days. We evaluated survivorship for this species with a larger sample size ($n = 77$ radiotagged birds) over a longer period of time ($n = 3$ yr) replicated across 3 study sites in southeastern Arizona. Our research overcame problems associated with radiotransmitter methods that were demonstrated in previous studies (Stromberg 1990, Hernandez et al. 2009). We made slight modifications to the transmitter design (standard backpack with loop-hole attachment to the wing), and evaluated it for its effect on quail movements and survival. Our modified design had no observable negative impact on flight ability nor reduced survival probabilities. Retrapping of birds seemed to have no significant impact on their survival. Potential impacts to Montezuma quail survival from trapping, such as exposing them to additional predation or increasing their risk of exposure to the elements from flushing them off roosts, was reduced by not trapping or flushing birds when increased predator activity or extreme departures from normal climate conditions were observed.

From telemetry data, we evaluated actual estimates of survival probability for the 3 study sites but could not evaluate estimates of survival for each study site each year. A large amount of censored data, attributed mostly to faulty transmitters (Chavarria 2013), resulted in smaller sample sizes at Stevens Canyon and Hog Canyon and prevented estimates of survival for those sites. This issue of faulty transmitters was resolved for the subsequent seasons. For all sites combined from autumn 2008 to autumn 2009, survival probability was low ($S = 0.219$). From winter 2009 to spring 2010, survival probability was extremely low at the AWRR ($S = 0.048$). Estimates of survival in our study were most accurate for results obtained at the AWRR study site. We did not calculate survival probabilities within the different sex and age classes for Steven's Canyon because of small sample size.

Log-rank Chi-square comparison of survival probabilities at the AWRR resulted in no significant differences between all variations comparing age and gender classes. The impact of right-censoring on inflating survival estimates is best observed for Steven's Canyon, where the survival estimate was extremely high and also included a large standard error ($S = 0.750$, SE $= 0.217$) and confidence interval (0.326–1.00). Such high survival probability is not very realistic for quail species for the study time frame. The survival estimate for Hog Canyon was more realistic ($S = 0.400$, SE $= 0.203$) but was inflated by birds that went unaccounted for and were censored from December to January during the hunting season. Some studies show that large variation in survival probability may be evident between seasons for some quail species (Terhune et al. 2007). On average, however, most studies on quail species similar to Montezuma quail, such as scaled quail (*Callipepla squamata*), mountain quail (*Oreortyx pictus*), and northern bobwhites (*Colinus virginianus*), reported survival probabilities that were considerably lower (Pleasant et al. 2006, Terhune et al. 2007, Stephenson et al. 2011, Troy et al. 2013) and resembled survival estimates in our study at the AWRR. The combined mean survival probability for all 3 sites from autumn 2008 to autumn 2009 is a more reliable estimate for the southeastern Arizona region and is comparable to survival probabilities observed for other North American quail species.

Most mortality of Montezuma quail is likely not attributable to hunting; natural factors relating to changes in habitat quality and climate probably create the biggest impact on their survival (Leopold and McCabe 1957, Yeager 1966, Heffelfinger and Olding 2000). This may be partly responsible for low survival probabilities listed for tagged birds at the AWRR from 2009 to 2010 following 2 stochastic events—a large and severe wildfire in May 2009 (Chavarria et al. 2012c) and a severe winter storm in winter 2009–2010 (Chavarria et al. 2012b). This is especially true for the winter storm because severe reductions in population abundances were documented across the 3 study sites in 2010 via both radiotelemetry and dog-assisted flush-count surveys (Chavarria et al. 2012b). Natural predation from avian predators such as red-tailed hawk (*Buteo jamaicensis*), Cooper's hawk (*Accipiter cooperii*), and great-horned owl (*Bubo virginianus*) likely accounts for the second greatest proportion of mortalities—especially of hatchlings and naïve juveniles—from early autumn to late winter (Stromberg 1990). Mortality from red-tailed hawk and Cooper's hawk was visually confirmed in this study.

Estimates of hunting mortality for this quail are likely to be higher than that reported in the literature, particularly when disease, stochastic events, and unfavorable environmental conditions (or a combination of those) combine with high season-specific harvest pressure to create additional stress to this species. Studies on bobwhite quail (Rolland et al. 2010) and other galliformes (Besnard et al. 2010, Sandercock et al. 2011) provide cautionary evidence to support this claim. Most literature on the impact of hunting mortality on Montezuma quail is based on evidence drawn from hunter surveys, counts of wings voluntarily submitted by hunters, check-station surveys, or estimates of abundances conducted from flush counts (Yeager 1966, Bristow and Ockenfels 2000, Heffelfinger and Olding 2000). Our study, however, also provides evidence of how censored data, resulting from unreported hunting mortalities that were later verified, artificially inflated survival estimates. Similarly, information drawn from hunter surveys, wing-counts, and check-stations are limited in many ways and thus reduce accuracy of estimating wild populations. Those data should be compared with data generated by more accurate means of estimating population abundances and densities, such as those provided by a combined use of flush-count surveys with monitoring via radiotelemetry.

MANAGEMENT IMPLICATIONS

Historical estimates of population abundances and densities of Montezuma quail in southeastern Arizona lack accuracy because there are insufficient data to account for rate of emigration and immigration between adjacent habitats or landscapes (i.e., canyons, mountain ranges). Hypothesized rate of recruitment and mortality derived from past studies, therefore, should be reevaluated. Without accurate estimates of range size and movements within a local area, one is at risk of overestimating the number of coveys in an area and thus overestimating the local population by double-sampling birds that move between adjacent hillsides, ravines, and patches of useable habitat. Stromberg (1990) cautioned that, because of Montezuma quail's high site fidelity and small use areas, "frequent and intense hunting pressure, particularly with trained bird dogs, can lead to virtual elimination of quail where hunter density is high, and thus should be considered as a conservation issue by land managers." Information from this research, especially that regarding estimates of Montezuma quail ranges, should be incorporated into future studies to more accurately evaluate actual rate of mortality throughout southeastern Arizona—with particular emphasis in areas where they are exposed to more frequent and intense anthropogenic pressures such as grazing and hunting.

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A PRESENCE–ABSENCE SURVEY TO MONITOR MONTEZUMA QUAIL IN WESTERN TEXAS

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ABSTRACT

Developing an effective monitoring program for Montezuma quail (*Cyrtonyx montezumae*) is challenging because the technique must be practical for surveying vast, remote landscapes while accounting for the species' low detectability. We used call-back surveys within a presence–absence framework to estimate occupancy and detection probability of Montezuma quail and used this information in conjunction with habitat data to develop an estimated probability of occurrence map for the species. We established survey points at 4 sites in western Texas ($n = 20$–30 points/site) and conducted 5 repeat surveys/season during June–August 2007 and 2008. We documented abiotic conditions (temperature, time of day, survey number, and year) during surveys and quantified microhabitat (% bare ground, food-plant density, vegetation height, and visual obstruction) and macrohabitat (vegetation type, elevation, aspect, and slope) at survey points. We then used an information-theoretic approach to evaluate the influence of micro- and macro-habitat on detection probability and occupancy at a local and regional scale, respectively. At a microhabitat scale, the most parsimonious model ($\Delta \mathrm{AIC}_c < 2$; Nagelkerke's $R^2 = 0.46$) suggested detection probability was influenced primarily by year ($\beta_{\mathrm{Year}} = 0.91$, 95% CI = 0.24–1.57), with occupancy being influenced primarily (but minimally) by year ($\beta_{\mathrm{Year}} = -59.7$, 95% CI = –179.0–59.6) and vegetation-height ($\beta_{\mathrm{VH}} = 67.7$, 95% CI = –71.9–207.4). This model indicated that detection probability decreased from 2007 (0.40; 95% CI = 0.31–0.49) to 2008 (0.21; 95% CI = 0.14–0.32), as did occupancy (1.00 vs. 0.72, respectively), which corresponded to a transition from a relatively wet to dry year. At a macrohabitat scale, the most parsimonious model ($\Delta \mathrm{AIC}_c < 2$; Nagelkerke's $R^2 = 0.20$) suggested occupancy was influenced by elevation ($\beta_{\mathrm{Elevation}} = 1.11 \pm 0.56$) and vegetation type ($\beta_{\mathrm{Vegetation\ type\ 2}} = -3.17 \pm 1.26$; $\beta_{\mathrm{Vegetation\ type\ 3}} = -1.20 \pm 1.18$), and we used these variables to construct a first-approximation, probability of occupancy map. Given our findings, presence–absence surveys may be a viable approach for monitoring Montezuma quail populations through time, and use of a probability of occupancy map can help with efficient allocation of survey points and effort. However, the viability of using a presence–absence approach to monitor Montezuma quail populations will depend on whether sampling effort can be increased sufficiently to obtain more precise estimates of occupancy. In addition, our probability of occupancy map should be regarded as a first approximation and further research should be conducted to refine the relationships.

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Key words: call-back surveys, *Cyrtonyx montezumae,* detection probability, Mearn's quail, occupancy modelling, predictive distribution map

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Montezuma quail (*Cyrtonyx montezumae*) is a species whose distribution occurs primarily in Mexico and reaches its northern limits in Arizona, New Mexico, and Texas. They inhabit perennial grasslands and oak woodlands and are one of the least known North American quail species because their secretive nature and cryptic plumage makes obtaining basic ecological information difficult (Brown 1989, Stromberg 2000, Hernández et al. 2006*a*, Harveson et al. 2007). This lack of ecological knowledge is problematic because the distribution and population size of Montezuma quail in Texas have declined over the past century, and the conservation status of the species is unknown despite it being a hunted species in the Southwest (Oberholser 1974, Gehlbach 1981, Harveson et al. 2007).

The practice of monitoring wildlife in order to manage their populations is a fundamental tenet of wildlife conservation and management (Leopold 1933). The cost of not having an effective monitoring program for species carries ecological, cultural, and political consequences (MacKenzie 2005). For example, although a general consensus exists that the geographic distribution of Montezuma quail has decreased and some local populations have become extirpated, no data exist on current densities, population trends, or contemporary distribution (Harveson et al. 2007), especially in Texas. Montezuma quail is a harvested species in Arizona and New Mexico but classified as a game bird but with no open season in Texas. In 2006, a proposal was presented in Texas to open a hunting season for the species but the proposition met considerable public resistance and eventually was withdrawn because of lack of supportive demographic data for the proposal.

Several challenges have impeded the development of an effective program for monitoring populations of Montezuma quail, such as their low detectability and occurrence on vast, remote landscapes. Traditional survey methods used for quail, such as whistling male counts, covey call counts, and roadside counts, do not work well with Montezuma quail because of their cryptic coloration, defense strategy of a tendency to crouch rather than flush, and infrequent calling (Harveson et al. 2007). Thus, researchers have attempted monitoring techniques such as "dig" counts, maps of foraging signs, line-drive techniques, radiotelemetry, and mark–recapture but have encountered limited success (Brown 1976, Bristow and Ockenfels 2000, Stromberg 2000, Robles et al. 2002, Hernández et al. 2006*b,* Harveson et al. 2007). However, recent theoretical advancements in monitoring techniques involving presence–absence data may provide a practical solution for reliably monitoring rare or elusive species over large scales (Thompson 2004, MacKenzie 2005). Geissler and Fuller (1987) proposed that data from repeated surveys could be used to estimate detection probabilities, and Azuma et al. (1990) demonstrated that repeated site visits could also be used to estimate occupancy while accounting for imperfect detection. The ability to obtain unbiased occupancy estimates has implications from a monitoring perspective because occupancy can be used as an index of population size, particularly for cryptic or low-density species, and occupancy estimation permits proper characterization of habitat models and resource selection functions (Vojta 2005, MacKenzie et al. 2006).

Call-back surveys have been used to monitor secretive bird species that are inconspicuous, inhabit dense cover, and/or are difficult to visually or aurally detect (Legare et al. 1999, Lor and Malecki 2002, Allen et al. 2004, and Conway and Gibbs 2005). Call-back surveys increase detection rates, decrease the proportion of survey points with no detections, and decrease coefficients of variation of population estimates beyond those of passive surveys (Allen et al. 2004, Conway and Gibbs 2005). For example, call-back surveys increased detection rates of 5 species of secretive marsh birds by factors of 2.4–7.0 over passive surveys (Allen et al. 2004). Thus, a monitoring program that used call-back surveys within an occupancy framework may provide a solution for monitoring Montezuma quail.

The purpose of our research was to evaluate a presence–absence approach using call-back surveys as a potential monitoring technique for Montezuma quail in western Texas. Our objectives were to 1) estimate occupancy rate and detection probability of Montezuma quail using call-back surveys, and 2) explore the development of a predictive distribution map for Montezuma quail in western Texas based on probability of occupancy as a function of habitat characteristics.

STUDY AREA

Our study was conducted on 4 study areas in western Texas: 1) Elephant Mountain Wildlife Management Area (Elephant Mountain WMA; Brewster County), 2) Davis Mountain Preserve of The Nature Conservancy (Davis MP; Fort Davis County), 3) a survey road route we called the Uvalde route (UVR; Uvalde, Real, Edwards, and Val Verde counties), and 4) a second survey road route we called the Del Rio route (DRR; Val Verde, Terrell, Pecos, and Brewster counties). The Elephant Mountain WMA and Davis MP were located within the Trans-Pecos Mountains and Basins ecoregion, whereas the Uvalde route was located within the Edwards Plateau ecoregion (Gould 1975). The Del Rio route was located in the transition zone between the Edwards Plateau and Trans-Pecos Mountains and Basins ecoregions.

Elephant Mountain Wildlife Management Area (Elephant Mountain WMA) is a 9,300-ha property of Texas Parks and Wildlife Department that was located approximately 40 km south of Alpine, Brewster County, Texas, USA (Hughes 1993, Hernández et al. 2006*b*). Elephant Mountain WMA has an elevation of 1,900 m and rises about 609 m above the surrounding lowlands (Hughes 1993). Mean annual precipitation ranged from 38 to 51 cm, with most of the precipitation occurring as summer monsoon rains during July–August. Soils varied in texture, and were developed from outwash materials from the surrounding mountains (Correll and Johnston 1979). The top of the mountain consists of an undulating plain that dips eastward and was dominated by desert grassland vegetation. The mesa drops off sharply along steep slopes, cliffs, and ledges to the surrounding lowlands. Vegetation on Elephant Mountain proper consisted of grasslands dominated by native grasses including sideoats grama (*Bouteloua curtipendula*), black grama (*B. eriopoda*), tobosa grass (*Pleuraphis mutica*), and bristlegrass (*Setaria* spp.). Woody vegetation was characterized by sparse patches of small shrubs including oak (*Quercus* spp.), mountain laurel (*Sophora secundiflora*), and fragrant sumac (*Rhus aromatica*) that were mostly associated with steep slopes, ravines, and the edges of exposed bedrock and talus (Hernández et al. 2006*b*).

The Davis Mountain Preserve (Davis MP) is an 11,500-ha nature preserve owned by The Nature Conservancy and located in Jeff Davis County, Texas (The Nature Conservancy 2006). The Davis MP is located approximately 40 km north of Fort Davis in the central region of the Davis Mountains. The Davis Mountains, along with the Guadalupe and Chisos mountains, form the "sky islands" of the Trans-Pecos Mountains and Basins ecoregion (Warshall 1995, DeBano and Ffolliott 2005). The Davis Mountains Preserve contains Mount Livermore, the second tallest peak in Texas at 2,225 m. Annual precipitation ranged from 28 to 57 cm, occurring mainly during the monsoon season (Jun–Sep). Soils were drained, hilly to steep, loamy, shallow to deep, and noncalcareous (Soil Conservation Service 1977). Dominant vegetation types were perennial grasslands, evergreen oak, oak–conifer woodlands, and oak–conifer forests. The Davis MP consists of a continuous extensive habitat for Montezuma quail; whereas, Elephant Mountain WMA is a small island habitat on top of Elephant Mountain proper. Perennial flowing drainages were common with alluvial soils and mountainous peaks that ranged in elevation from 1,500 to 2,200 m (King 2003). The Davis MP has not been grazed by livestock since its purchase in the early 1990s, but is grazed by native herbivores including elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*). The Davis MP has reintroduced fire to the Davis Mountains ecosystem to reduce heavy fuel loads and catastrophic wildfire threats and to mimic natural ecosystem processes (The Nature Conservancy 2006).

The Uvalde route (UVR) was a road route that included the following counties: Uvalde, Real, Edwards, and Val Verde. The UVR began outside of Leaky, Texas, on Ranch Road 337 and ran due west to Campwood, Texas. It continued north along Ranch Road 55 to Rocksprings, Texas, where it joined Ranch Road 337 to Carta Valley, Texas. Upon reaching Highway 227, it continued due south on Highway 227 until reaching Del Rio, Texas. The area surveyed included counties that are known for sheep–goat–cattle operations (Albers and Gehlbach 1990). The Edwards Plateau ecoregion was an uplifted and elevated region originally formed from marine deposits of sandstone, limestone, shales, and dolomites 100 million years ago during the Cretaceous Period when this region was covered by an ocean (Texas Parks and Wildlife Department 2007*a*). The Edward Plateau was composed primarily of grassland savanna with shrubs and low trees along rocky slopes and drainages (Correll and Johnston 1970, Stanford 1976, Weniger 1988, Hatch et al. 1990, Baccus and Eitniear 2007). Before European settlement, recurrent fires suppressed woody plants and maintained the open, grassy nature of the landscape on relatively level ground but not on steeper slopes and canyon walls (Weniger 1988, Baccus and Eitniear 2007). However, European settlement resulted in livestock overgrazing and the depletion of grasses and their replacement by less desirable woody shrubs (Schmidly 2002). Many of the plants found in the Edwards Plateau included oaks (*Quercus* spp.), ashe and redberry juniper (*Juniperus* spp.), mesquite (*Prosopis* spp.), lotebush (*Ziziphus obtusifolia*), yucca (*Yucca* spp.), pricklypear (*Opuntia* spp.), persimmon (*Diospyros* spp.), hackberry (*Celtis* spp.), catclaw (*Acacia* spp.), pricklyash (*Zanthoxylum* spp.), and sumac species (*Rhus* spp.) that contributed to habitat for many wildlife species as food and cover (Texas Parks and Wildlife Department 2007*a*).

The Del Rio Route (DRR) was a roadside route that surveyed the transition from the Edwards Plateau ecoregion into the Trans-Pecos Mountains and Basins ecoregion and included the following counties: Brewster, Pecos, Terrell, and Val Verde. The DRR consisted of a stretch of road on Highway 90 from Alpine, Texas to Del Rio, Texas. This transition zone consisted of low-elevation desert shrublands that transitioned into high-elevation desert grasslands and mountains. This unique combination contributed to tremendous vegetation diversity in the region that included $\geq$268 grass species and 447 species of woody plants (Texas Parks and Wildlife Department 2007*c*). However, the vegetation and wildlife has changed dramatically during the past 120 years as a result of drought, livestock grazing, and suppression of fire (Texas Parks and Wildlife Department 2007*c*). Prominent invaders of the low-elevation desert shrublands and grasslands included creosotebush (*Larrea tridentata*), tarbush (*Flourensia cernua*), whitethorn acacia (*Vachellia constricta*), mesquite, and cacti (*Opuntia* spp.). Prominent invaders of the higher elevation plains included catclaw (*Senegalia. greggii*), sacahuista (*Nolina microcarpa*), cane cholla (*Cylindropuntia imbricata*), broom snakeweed (*Gutierrezia sarothrae*), and prickly pear species (Texas Parks and Wildlife Department 2007*c*). The DRR traversed 13 vegetation types including creosotebush–tarbush shrub, creosotebush–mesquite shrub, creosotebush–lechuguilla (*Agave lecheguilla*), or cenizo (*Leucophyllum frutescens*)–blackbrush (*Acacia rigidula*)–creosotebush (Texas Parks and Wildlife Department 2007*c*).

METHODS

Occupancy and Probability of Detection

Survey points.—We conducted call-back surveys during July–August 2007 and June–August 2008 only at Elephant Mountain WMA and Davis MP. In 2008, we added the UVR and DRR road routes to obtain a wider representation of vegetation communities within the ecoregion and species' geographic distribution. We chose June–August to conduct surveys because these months represent the approximate occurrence of the monsoon rains in the Trans-Pecos Mountains and Basins ecoregion and corresponded to the period of peak calling by Montezuma quail (D. Holdermann, Texas Parks and Wildlife Department, unpublished report).

We selected survey points at Elephant Mountain WMA and Davis MP in 2007 by overlaying a 400 × 400-m^2 grid over a map of each respective study area using geographic information systems (GIS) and ArcGIS® 9.2. We chose a 400 × 400-m^2 grid based on Bishop (1964), who stated that the approximate radius of audibility of a male Montezuma quail buzz call was approximately 200 m. Each grid was given a numbered centroid, and we randomly selected 30 survey points using Microsoft Office Excel 2003® (Microsoft, Redmond, WA, USA). In 2008, we increased the grid size (800 × 800-m^2) to minimize the probability of double-counting. This increase in grid size resulted in fewer points occurring within the original monitoring area. First year results indicated complete occupancy within our original monitoring area, so we placed the "extra" points in new, surrounding areas to include suboptimal habitat. We defined suboptimal habitat as vegetation communities where Montezuma could be found but were not the preferred community (i.e., oak woodland). The placement of these extra points was stratified by vegetation community within this suboptimal category. Such a change was designed to increase the range of occupancy and diversity of vegetation types surveyed and therefore provide better habitat data for modeling occupancy and detection probability. We were able to retain 14 of the original 30 points at Elephant Mountain WMA, resulting in 16 points being placed in suboptimal habitat still within Elephant Mountain WMA. At Davis MP, we were able to retain 10 of the original 30 survey points; the other 20 points had to be placed in areas outside of Davis MP. Eight of these new points were located on Highway 118 north between Alpine, Texas and Fort Davis, Texas. Three more points were located on Highway 17 due south of Fort Davis and the remaining 9 points were located on Highway 17 due north of Fort Davis. For DRR and UVR, we used the vegetation-types map of Texas Parks and Wildlife Department to select survey points along roads. We established 5 survey points/vegetation type on DRR ($n = 20$ survey points) and UVR ($n = 25$ survey points). We allocated survey points with the goal of sampling as many vegetation types as logistically possible.

Call-back surveys.—We used a playback recording of a male buzz call or combination of a male buzz call and a covey-assembly call to detect presence (S. Sorola, retired wildlife biologist, Texas Parks and Wildlife Department, personal communication). Call-back surveys consisted of playing the recording for 1.5 minutes with a 30-second pause to listen for a Montezuma quail response. If no calls were heard, we continued to play the call for 30 seconds more followed by a 30-second pause. We repeated this call-back protocol for 5 minutes. We recorded the number of individuals calling and total calls heard for each survey. We also recorded survey date, time of day, temperature, humidity, and wind speed during each survey. We measured temperature, humidity and wind speed using a Kestrel 3000 wind meter (Nielsen-Kellerman Co., Boothwyn, PA, USA). We conducted repeat surveys at each point 5 times during each field season. Thus, annual survey effort for Elephant Mountain WMA and Davis MP was 150 surveys (30 sites × 5 visits) each. Annual survey effort was 100 surveys (20 sites × 5 visits) for DRR and 125 surveys (25 sites × 5 visits) for UVR. The ability to detect Montezuma quail could vary throughout the day; therefore, we conducted call-back surveys at different times of the day during the repeated visits. We partitioned the daylight period into 2 categories: morning (0700–1100 hr) and evening (1600–2000 hr). We randomly chose points to be surveyed for a given time period with the stipulation that all survey points had to be surveyed before an individual point was sampled again.

Weather.—We obtained daily and monthly precipitation and temperature data for Elephant Mountain WMA and Davis MP during May–August 2007 and 2008 using PRISM (Parameter-elevation Relationships on Independent Slopes Model, Oregon State University; http://www.prism.oregonstate.edu/). We selected the center-most 4 × 4-km PRISM grid cell that fell within the boundary of each site and used the interpolation option to allow values to be adjusted for surrounding cells. We did not obtain weather data for DRR and UVR because these routes were not contained within a delineated study area but rather distributed across ≈480 km of roads throughout the ecoregion. Thus, survey points were spaced too far apart for a meaningful regional, interpolation of weather.

Vegetation Sampling

Microhabitat.—We quantified 2 broad categories comprising microhabitat (i.e., structure and food resources) at survey points at Elephant Mountain WMA and Davis MP. We did not measure microhabitat at survey points comprising DRR and UVR because these points occurred along public county roads that were bordered by private property, and thus we had restricted access. Variables quantifying vegetation structure consisted of percent herbaceous coverage (percent litter, forb, grass, and bare ground), vegetation height, and visual obstruction that were measured using a Daubenmire frame (Bonham et al. 2004), Robel pole (Robel 1969), and vegetation profile board (Nudds 1977), respectively.

We established 4 30-m transects at each point radiating in the 4 cardinal directions. We measured vegetation structure at the 10-m, 20-m, and 30-m mark along each transect. For herbaceous coverage, we visually estimated percent litter, forb, grass, and bare ground using a Daubenmire frame (20 cm × 50 cm). We obtained vegetation height readings using a Robel pole from a 4-m distance at 1-m height in each of the 4 cardinal directions (Robel 1969). In addition, we estimated visual obstruction for each of 4-dm strata (0–10, 10–20, 20–30, 30–40) using a profile board following the protocol used for vegetation height (4-m distance, 1-m height, 4 cardinal directions; Nudds1977). We determined food-plant density using a 1- × 1-m frame at 10-m, 20-m, and 30-m plots along each transect. We recorded the number of individual plants of *Allium* spp., *Oxalis* spp., and *Cyperus* spp., and calculated food-plant density from these data (Hernández et al. 2006*b*).

Macrohabitat.—We measured macrohabitat variables such as aspect, elevation, slope, and vegetation type at survey points at all 4 sites. We determined aspect and elevation using ArcGIS® 9.2. Aspect was given a north, east, south, or west direction depending on the direction the mountain slope faced. Elevation (m) data were collected from ArcGIS™ Digital Elevation Model at a 1-km resolution from the Universal Transverse Mercator projected coordinate WGS 1984 UTM ZONE 14. We determined slope (°) using a Suunto® KB-14 clinometer (Shreveport, LA, USA). For areas to which we did not have access (i.e., roadside survey points), we obtained slope using ArcGIS™ 3D™ analyst, which is a three-dimensional visualization, topographic analysis, and surface creation. We also classified each point into a habitat-type category based on the Vegetation Types of Texas map of Texas Parks and Wildlife Department (Texas Parks and Wildlife Department 2007*b*). The study area encompassed 13 vegetation types. We consolidated these 13 vegetation types into 3 habitat-category types (high, moderate, and low) in order to reduce the number of covariates used in habitat modeling. Categorization was based on our field experience and knowledge of these vegetation communities to serve as Montezuma quail habitat and the degree of similarity between the vegetation characteristics associated with a particular vegetation type and known characteristics of Montezuma quail habitat (Brown 1978, Harveson et al. 2007). Habitat-category high consisted of the following vegetation types: 1) gray oak (*Q. grisea*)–pinyon pine (*Pinus edulis*)–alligator juniper (*J. deppeana*) parks andwoods, and 2) live oak (*Q. wislizeni*) –ashe juniper (*J. ashei*) parks. Habitat-category moderate consisted of the following vegetation types: 1) cenizo–blackbrush–creosote bush, 2) creosotebush–lechugilla shrub, 3) live oak–juniper woods, 4) live oak–mesquite–ashe juniper, 5) mesquite–juniper shrub, and 6) mesquite–juniper–live oak brush. Finally, habitat-category low consisted of the following vegetation types: 1) creosote–mesquite shrub, 2) creosote–tarbush shrub, 3) mesquite–blackbrush brush, 4) tobosa–black grama grassland, and 5) yucca–ocotillo (*Fouquieria splendens*) shrub.

Statistical Analysis

Calling phenology.—Montezuma quail calling is closely tied with precipitation, with calling generally peaking within a few days following rainfall and rapidly declining thereafter (Brown 1978, Harveson et al. 2007). In addition, high summer temperatures can have suppressive effects on calling. Thus, we calculated mean weekly calling rates (no. of birds calling per point per week) to correlate with mean weekly precipitation or mean maximum temperature. We defined weeks as follows: 1 (24 Jun–30 Jun), 2 (1 Jul–7 Jul), 3 (8 Jul–14 Jul), 4 (15 Jul–21 Jul), 5 (22 Jul–28 Jul), 6 (29 Jul–4 Aug), 7 (5 Aug–11 Aug), 8 (12 Aug–18 Aug), and 9 (19 Aug–25 Aug) for 2007 and 2008. We partitioned precipitation and temperature data into these same weekly periods. We conducted a Pearson Correlation analysis in Program SAS between mean weekly calling rates (no. birds calling per point per week) and either mean weekly precipitation (mm) or mean maximum daily temperature (° C).

Occupancy and detection probability.—Prior to conducting any analysis in Program MARK (White and Burnham 1999), we conducted a Pearson Correlation Matrix in Program SAS on all explanatory variables (i.e., 13 microhabitat variables and 4 macrohabitat variables). For variable pairs that were highly correlated ($r \geq 0.60$), we kept the most biologically relevant (i.e., greatest relevance to the species from an ecological or management perspective) variable and eliminated the other from the data set. From this reduced set of explanatory variables, we then built a set of 29 *a priori* models with biological relevance to evaluate the influence of habitat structure, food resource, and year on occupancy and detection probability. Specifically, these models evaluated occupancy as a function of year, herbaceous cover, vegetation height, and food-plant density, and evaluated detection probability as a function of year, survey number, time of day, and vegetation height. In this analysis, we only used points for which we had data for both 2007 and 2008 (i.e., points sampled in both years; $n = 24$ points) because our objective was to document how occupancy fluctuated through time over a common area. We modeled occupancy and probability of detection simultaneously (P. Doherty, Colorado State University, personal communication); that is, we modeled a particular detection model with each possible occupancy model. We used Akaike's Information Criterion (AIC_c) to identify the best model ($\Delta AIC_c < 2$) and calculated a pseudo-R^2 statistic for each model to assess how much variation was explained (Nakagawa and Schielzeth 2013).

Predictive distribution map.—We developed 9 *a priori* models to evaluate the influence of macrohabitat on occupancy for development of a probability of occupancy map. These models evaluated occupancy as a function of aspect, slope, elevation, and habitat-category type. We used data from all 4 sites collected during July–August 2008 for this analysis: Elephant Mountain WMA ($n = 30$ survey points), Davis MP ($n = 30$ survey points), UVR ($n = 25$ survey points), and DRR ($n = 20$ survey points). We used Akaike's Information Criterion (AIC_c) to identify the best model and calculated a pseudo-R^2 statistics for each model to assess how much variation was explained (Nakagawa and Schielzeth 2013). We then used the best model to develop a predictive occupancy map using ArcGIS® 9.3 and ERDAS® Imagine Model Maker (Hexagon Geospatial, Madison, AL, USA).

RESULTS

Weather and Calling Behavior

General weather conditions were relatively drier and hotter at Elephant Mountain WMA compared with Davis MP, an expected observation given the higher elevation of Davis MP. Mean monthly rainfall was lower at Elephant Mountain WMA during May–July 2007 (range = 33–72 mm) and May–July 2008 (range = 19–57 mm) compared

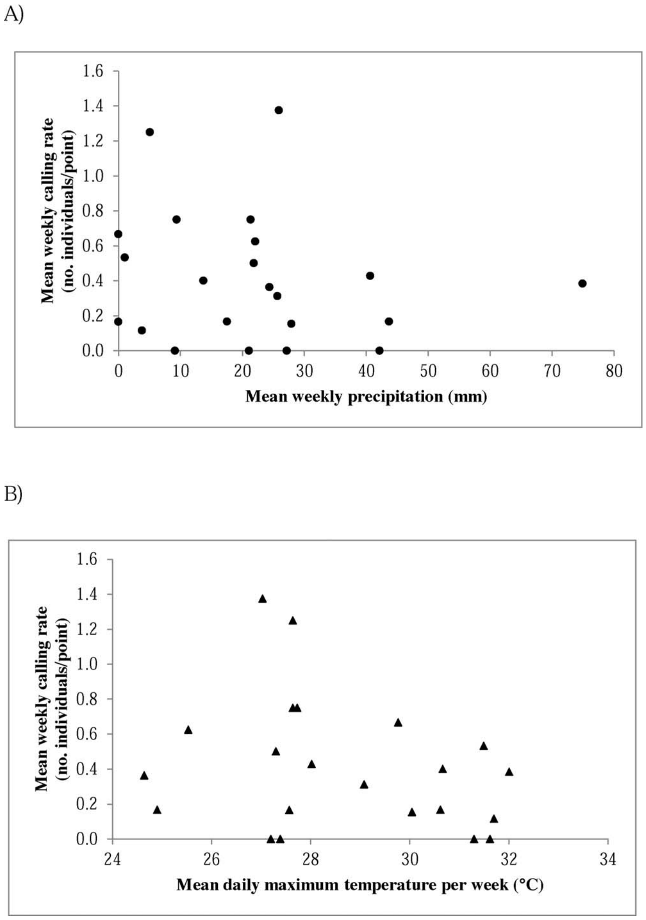

Fig. 1. Scatterplot of mean weekly calling rate (no. of individuals heard per point) of Montezuma quail and (A) mean weekly precipitation (mm), and (B) mean maximum daily temperature per week (° C), Brewster and Jeff Davis counties, Texas, USA, June–August 2007 and 2008.

with Davis MP (range = 64–98 mm and 6–149 mm, respectively). Mean maximum daily temperature was higher at Elephant Mountain WMA during May–July 2007 (range = 23–26° C) and May–July 2008 (range = 25–30° C) compared with Davis MP (range = 17–21° C and 19–24° C, respectively). Weather conditions tended to be drier and hotter during the second year. Mean monthly precipitation (May–Jul) decreased from 2007 to 2008 at both Elephant Mountain WMA (54 mm vs. 35 mm, respectively) and Davis MP (82 mm vs. 71 mm, respectively). Mean maximum daily temperature (May–Jul) increased from 2007 to 2008 at both Elephant Mountain WMA (25° C vs. 27° C, respectively) and Davis MP (19° C vs. 21° C, respectively).

The change to more xeric conditions during the second year of study was reflected in a corresponding decrease in calling rates. Mean weekly calling rates decreased by 50% from 2007 (0.4 ± 0.1 birds calling/point) to 2008 (0.2 ± 0.1 birds calling/point) at Elephant Mountain WMA. We also observed a 66% decrease in mean weekly calling rates from 2007 (0.6 ± 0.1 birds calling/point) to 2008 (0.2 ± 0.1 birds calling/point) at Davis MP. However, when we evaluated whether mean weekly calling rate closely tracked mean weekly precipitation within a given year, we observed no correlation during 2007 ($r = –0.04$, $P = 0.88$) or 2008 ($r = 0.14$, $P = 0.71$; Fig. 1A). Similarly, mean weekly calling rate and mean maximum daily temperature were not correlated during 2007 ($r = –0.55$, $P = 0.07$) or 2008 ($r = –0.27$, $P = 0.46$), although the relationship approached significance during 2007 (Fig. 1B).

Occupancy and Probability of Detection

We evaluated 29 *a priori* microhabitat models using AIC_c to assess the influence of 1) habitat structure and food resources on occupancy, and 2) habitat structure and survey characteristics on detection probability. The most parsimonious model ($\Delta AIC_c < 2$; Nagelkerke's $R^2 = 0.46$) suggested occupancy was influenced primarily (but minimally) by year ($\beta_{Year} = –59.7$, 95% CI = –179.0–59.6) and vegetation-height ($\beta_{VH} = 67.7$, 95% CI = –71.9–207.4), whereas detection probability was influenced by year ($\beta_{Year} = 0.91$, 95% CI = 0.24–1.57; Table 1). Occupancy rates decreased from 2007 (1.00) to 2008 (0.72; 95% CI = 0.00–1.00), although the precision of occupancy estimates decreased considerably during the second year. In addition, vegetation height positively influence probability of occupancy, with a greater threshold value for vegetation height required for occupancy during 2008 (Fig. 2). Detection probability decreased from 2007 (0.40; 95% CI = 0.31–0.49) to 2008 (0.21; 95% CI =0.14–0.32).

Predictive Distribution Map

We evaluated 9 *a priori* macrohabitat models using AIC_c to develop a predictive map of occupancy. These models evaluated occupancy as a function of aspect, slope, elevation, and habitat-category type. The most parsimonious model ($\Delta AIC_c < 2$; Nagelkerke's $R^2 = 0.20$) suggested occupancy was positively influenced by elevation ($\beta_{Elevation} = 1.11$, 95% CI = 0.0 ± 2.23) and habitat-category type (Table 1). Increasing elevation increased the probability of occupancy within all habitat-category types (Fig. 3). We used this model to construct a probability of occupancy map to include areas that were adjacent to the historical or known Montezuma quail distributions (Fig. 4). The map generally coincided with our field knowledge of Montezuma quail distribution but there were a few counties where the probability of occupancy appeared relatively higher (Maverick and Zavala) or lower (northern Edwards) than field knowledge indicated.

DISCUSSION

We documented that calling activity, occupancy, and probability of detection of Montezuma quail decreased as weather conditions changed from wet (2007) to dry (2008). We also documented that occupancy was influenced by vegetation height and year at a local level and elevation and habitat-category at a regional scale. Below we discuss the ecological relevance of these

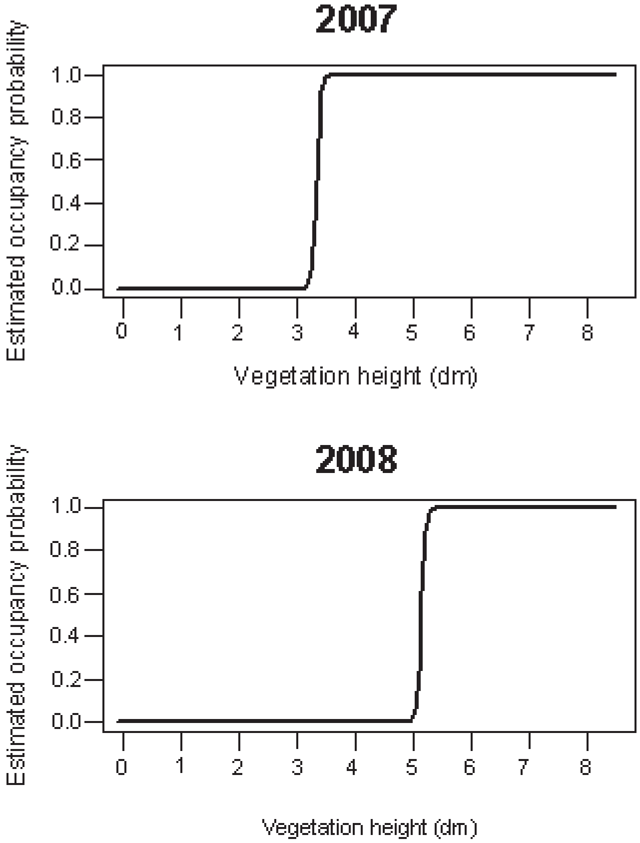

Fig. 2. Predicted probability of occupancy of Montezuma quail as a function of vegetation height (dm), Brewster and Jeff Davis counties, Texas, USA, June–August 2007 and 2008.

findings and how they may be used to develop a monitoring technique for Montezuma quail.

Weather and Calling Behavior

We observed that a transition to more xeric conditions during our study negatively impacted calling behavior of Montezuma quail. Environmental conditions became hotter and drier from 2007 to 2008 and calling activity decreased correspondingly. These findings are consistent with past research documenting the general phenomenon of the suppressive effects of droughty conditions on quail behavior and populations (Heffelfinger et al. 1999, Guthery et al. 2002, Lusk et al. 2002). In contrast, although we observed a general relationship between dry conditions and calling behavior between years, we did not document a correlation between weekly calling rate and weekly precipitation or temperature within a given year. This finding is inconsistent with what has been reported for Montezuma quail and other quail species. Precipitation is known to be associated with reproductive behavior (e.g., calling, breeding, and nesting) of Montezuma quail (Stromberg 2000). For example, Brown (1979) stated a positive correlation existed between summer precipitation and Montezuma quail harvest. Stromberg (1990) reported that nesting occurred after rains in July and August that resulted in green vegetation. Moreover, Bishop and Hungerford (1965) noted that the herbaceous plants that provide the major winter food items for Montezuma quail, (e.g., *Allium* spp., *Oxalis* spp., and *Cyperus* spp.) are products of summer precipitation. The lack of an apparent relationship between weekly calling and weekly measures of weather in our study may have resulted from weather data being collected at a coarse resolution. The weather data we used for the analysis was obtained from PRISM, which predicts precipitation and temperature values using climate–elevation regression models and incorporates factors such as location, elevation, coastal proximity, topographic facet orientation, vertical atmospheric layer, topographic position, and orographic effectiveness of the terrain (Daly et al. 2008). Thus, actual weather at our study sites and those predicted by PRISM may have differed, resulting in low correlation between weather and calling activity of Montezuma quail on a weekly temporal scale.

Occupancy and Probability of Detection

Occupancy and probability of detection also decreased from 2007 to 2008 with increasing xeric conditions. Occupancy appeared to be influenced primar-

Table 1. Top ranked models for occupancy and probability of detection of Montezuma quail based on micro- and macrohabitat characteristics, Brewster and Jeff Davis counties, Texas, USA, June–August, 2007 and 2008. Criterion corrected for sample size (AIC$_c$), number of model parameters (K), difference in AIC$_c$ relative to best model (ΔAIC$_c$), model likelihood, model weight (w), and Nagelkerke's pseudo-R^2 values are shown.

Variable model	K	AIC$_c$	ΔAIC$_c$	w	Pseudo R^2
Microhabitat					
Ψ(year + vegetation height), p(year)	5	241.13	0.00	0.60	0.46
Ψ(year + grass cover), p(year + vegetation height)	6	244.72	3.60	0.10	0.44
Ψ(year + vegetation height + food-plant density), p(year + survey)	7	244.77	3.64	0.10	0.47
Ψ(year + grass cover), p(year)	5	245.74	4.62	0.06	0.40
Ψ(year + grass cover), p(year + survey + vegetation height)	7	246.38	5.25	0.04	0.45
Macrohabitat					
Ψ(elevation + habitat category), p(.)	5	221.32	0.00	0.41	0.20
Ψ(elevation + aspect + habitat category), p(.)	6	221.60	0.28	0.36	0.21
Ψ(elevation + slope + habitat category), p(.)	6	223.31	2.00	0.15	0.20
Ψ(habitat category), p(.)	4	226.72	5.40	0.03	0.13
Ψ(slope + habitat category), p(.)	5	227.01	5.70	0.02	0.15

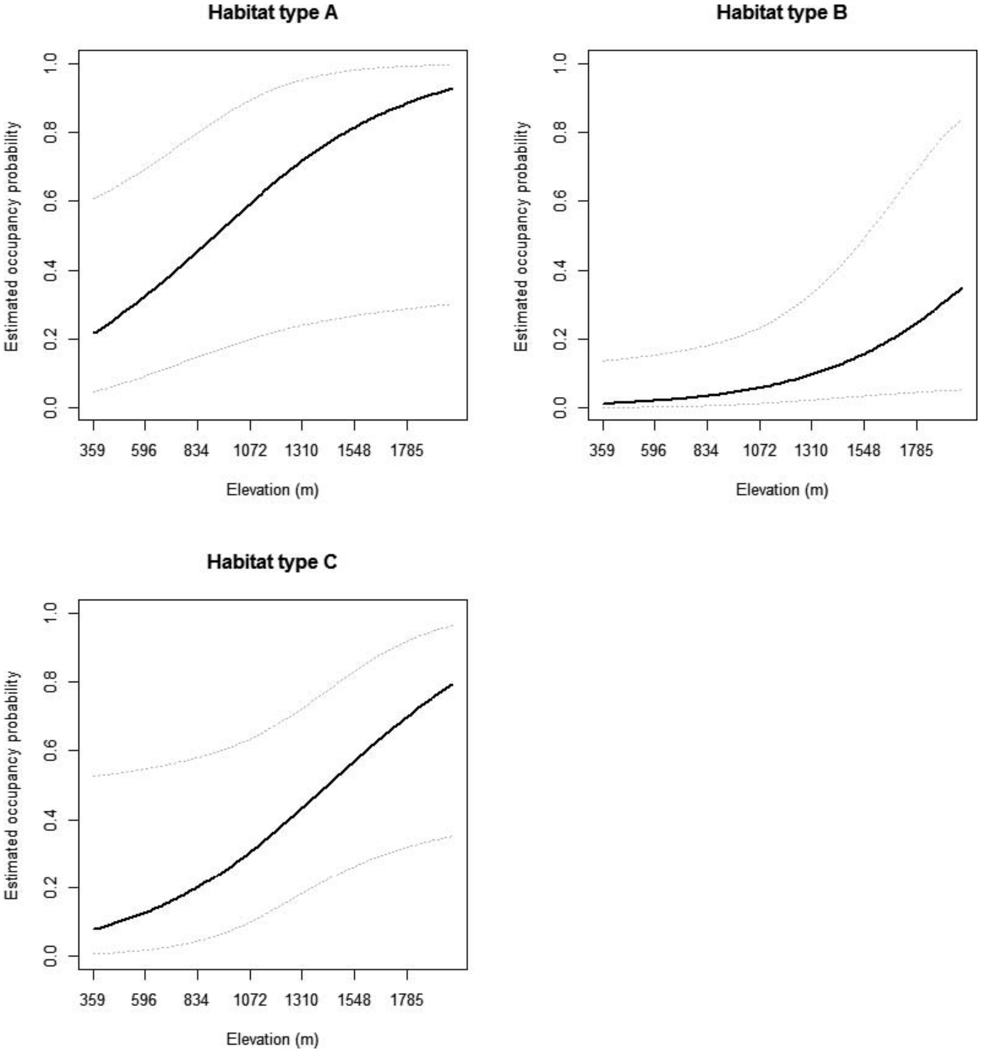

Fig. 3. Predicted probability of occupancy of Montezuma quail as a function of elevation and habitat-category type in western Texas based on presence–absence data collected in Brewster, Edwards, Jeff Davis, Pecos, Real, Terrell, Uvalde, and Val Verde counties, Texas, USA, June–August 2008.

ily (but minimally) by year and vegetation height, whereas detection probability appeared to be influenced by year. Our observation of a positive influence of vegetation height on occupancy is consistent with the ecology of the species. The importance of herbaceous cover for Montezuma quail is well-established (Leopold and McCabe 1957; Bishop 1964; Brown 1978, 1982). Bristow and Ockenfels (2004) noted that cover availability is an important factor affecting Montezuma quail distribution and density and that factors that reduce this cover such as livestock overgrazing detrimentally impact the species. Albers and Gehlbach (1990) also documented that large amounts of tallgrass cover predicted feeding habitat of Montezuma quail on both grazed and nongrazed areas and were most important during the summer months, the time of our study. Furthermore, Bristow and Ockenfels (2002, 2004) reported that vegetation richness, visual obstruction, and cover affected habitat selection during the brood season.

One general finding of ecological interest is that we documented relatively high occupancy at both Elephant Mountain WMA and Davis MP, 2 study sites that vary considerably in vegetation structure. The vegetation community at Elephant Mountain proper consists primarily of a blue grama–dominated grassland with brush cover limited to the edges of the mesa along steep slopes and ravines. In contrast, the Davis MP is the quintessential habitat of Montezuma quail and consists of pinyon–juniper woodlands and forests (Sanders 2012). This finding of high occupancy at these 2 sites suggests that Montezuma quail may have wide habitat-suitability bounds given that the 2 study areas are markedly different in plant-species composition and structure (Sanders 2012). In general, Elephant Mountain WMA tended to have a less forb cover (6%), lower vegetation height (2 dm), but more grass cover (41%) compared with Davis MP (13%, 4 dm, and 33%, respectively; Sanders 2012). Bristow and Ockenfels (2004) reported that Montezuma quail prefer oak–woodland communities with $\geq$26% tree canopy cover and 51–75% grass cover but can exist in areas with relatively few oak trees, although quail densities are often lower than typical in oak–woodland

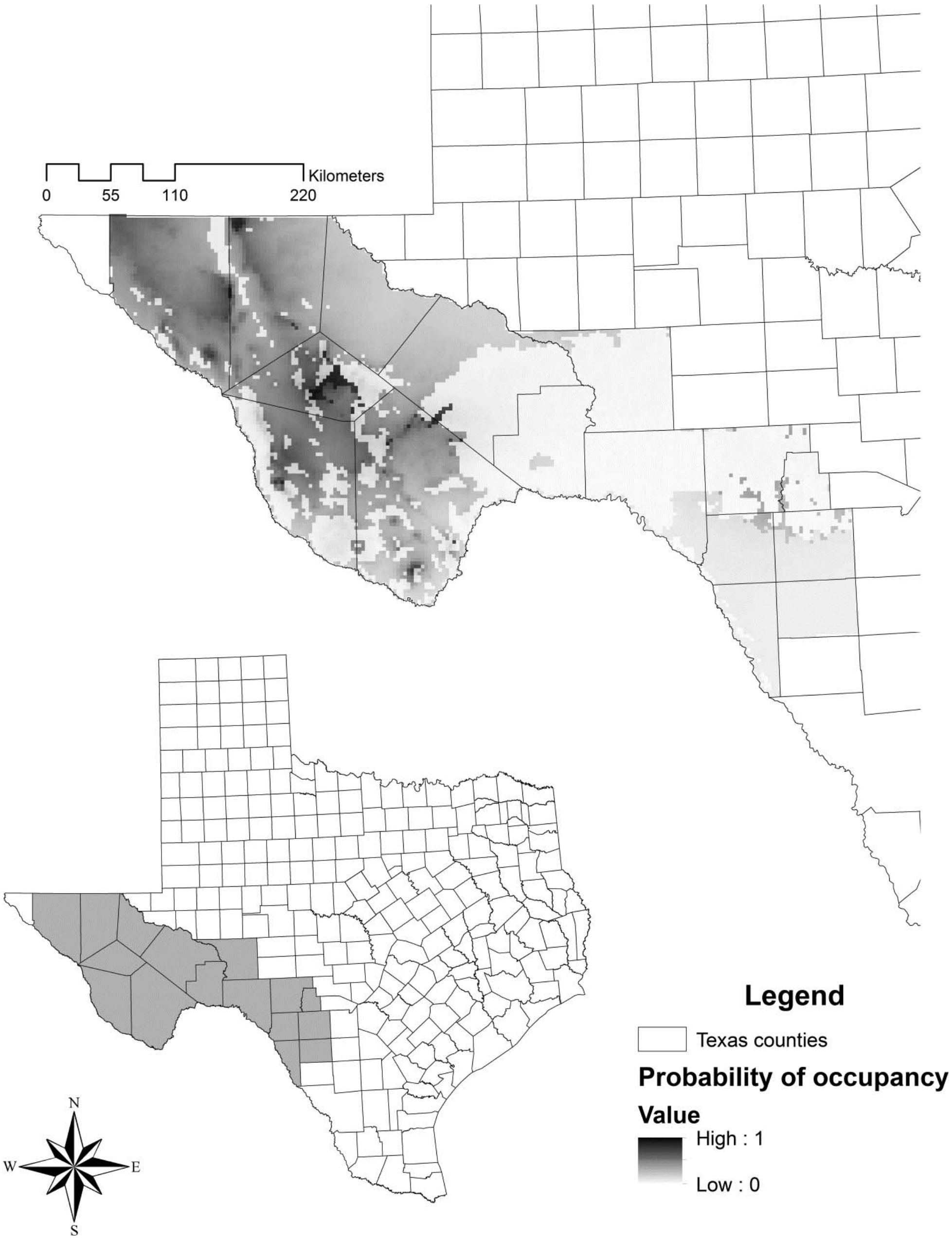

Fig. 4. Map of probability of occupancy of Montezuma quail for western Texas based on presence–absence data collected in Brewster, Edwards, Jeff Davis, Pecos, Real, Terrell, Uvalde, and Val Verde counties, Texas, USA, June–August 2008.

habitat. Thus, although occupancy of Montezuma quail was high at both Elephant Mountain WMA and Davis MP, density still may have differed between the 2 areas. Nevertheless, it appears that habitat structure near ground level may be more important than habitat structure of the overstory or general plant-species composition in determining habitat suitability for Montezuma quail. Hernández et al. (2006*b*) believed that general plant-species richness and diversity did not adequately characterize foraging habitat for Montezuma quail because of their specialized diets. On our study area, Sanders (2012) documented that Montezuma quail were found in areas with $\geq$6.5% forb cover and $\approx$2.7 food plants/m^2. Collectively, these findings suggest that areas varying in overstory habitat structure and general plant-species diversity may be capable of supporting Montezuma quail populations if sufficient grass cover and their key food-plant species (e.g., *Allium* spp., *Oxalis* spp., *Cyperus* spp.) are present.

Predictive Distribution Map

We documented that elevation and habitat-category type (high, moderate, or low) influenced probability of occupancy at a regional scale in our exploratory analysis. The elevation of survey points at Elephant Mountain WMA ranged from 1,596 to 1,896 m in 2007 and from 1,325 to 1,896 m in 2008. At Davis MP, the elevation of survey points ranged from 1,770 to 2,012 m in 2007 and from 1,144 to 1,992 m in 2008. Elevation varied between years because survey points changed between field seasons with the expansion of our study area to include suboptimum habitat within these 2 sites. The importance of elevation for presence of Montezuma quail has been noted by various researchers. For example, Garza (2007) reported that elevations of Montezuma quail sightings at the Davis MP were most common from 1,738 to 1,838 m. Leopold and McCabe (1957) documented sightings at 1,554 to 2,286 m, while Stromberg (2000) documented nests at elevations from 1,520 to 1,920 m. Hernández et al. (2006*b*) found Montezuma quail at elevations of approximately 1,900 m. Naturally, it is not likely that elevation *per se* determines Montezuma quail presence but rather the influence of elevation as exerted on climate and vegetation communities that result in favorable habitat for the species.

Regarding the relative accuracy of the predictive distribution map, the map generally coincided with field knowledge and known occurrence of Montezuma quail, although some discrepancies were present. Areas of high probability of occupancy corresponded to areas near Elephant WMA, Davis MP, and Presidio, Texas. These regions of high probability of occupancy coincided closely with the current distribution map reported by Harveson et al. (2007). However, there were a few locations where the probability of occupancy appeared relatively higher (Maverick and Zavala counties) or lower (northern Edwards County) than current field knowledge indicated. The incongruence may have resulted from survey data for these areas being collected along roads and/or a low sampling intensity. Although roadside surveys occurred in remote areas with low-traffic roads, the data of roadside surveys may have differed from data collected within large interior tracts of habitat. Another possibility is that the sampling intensity of survey points within each of the 16 vegetation types (5 survey points/vegetation type) was not sufficient to adequately capture variation in occupancy. In addition, we had to consolidate these diverse vegetation types into a smaller subset (3 habitat-category types) for statistical analysis. Such pooling not only reduced the level of precision possible for a probability of occupancy map developed using presence–absence data from all 16 vegetation communities, but it also introduced nuisances associated with pooling. For example, the yucca–ocotillo shrub vegetation community generally is characterized by a hot, arid environment and thus is not considered typical Montezuma habitat. Thus, we categorized this vegetation type as habitat-category low. However, this vegetation type at Elephant Mountain WMA occurs at relatively high elevation and adjacent to the mountain proper where Montezuma quail habitat exists. At this site, Montezuma quail on the mountain proper often venture to the slopes and foothills and sometimes are found in the yucca–ocotillo shrub vegetation type. Thus, in general, the yucca–ocotillo shrub vegetation type would be classified as habitat-category low but is a habitat-category moderate at Elephant Mountain WMA because of its elevation and location adjacent to Montezuma habitat. These fine-level considerations on a site by site basis would need to be considered and incorporated to increase the accuracy of a probability of occupancy map on region-wide scale, which would be a plausible but time-consuming task.

We emphasize that the habitat-occupancy relationships developed both at the micro- and macrohabitat scale represent an exploratory analysis and should be interpreted as such. These relationships are limited by low precision of occupancy rates and relatively low sampling intensity of vegetation characteristics. In addition, a mismatch of scale exists between microhabitat variables (collected within 30 m of survey points) and occupancy (estimated within 800 m of survey points). Thus, although the findings of these exploratory analyses closely align with the ecology of the species, these results should be viewed as preliminary and further research is necessary to refine the habitat-occupancy relationships.

Survey Potential

We observed that occupancy fluctuated through time in accordance with environmental conditions. Such fluctuations are similar to the population fluctuations observed for other quail species that are indexed via roadside counts conducted by state agencies (DeMaso et al. 2002). This suggests that is possible for general population trends of Montezuma quail to be tracked via occupancy estimation through time. However, although this certainly is encouraging, we also observed that the precision of occupancy estimates varied depending on environmental conditions. We observed relatively high precision of occupancy during a relatively mesic year (2007), but poor precision during a more xeric year (2008). This limitation of decreased precision during dry years would need to be addressed for development of meaningful population trends, a limitation that could be remediated by increasing survey effort. Using probability laws and an average probability of calling of 0.30, it was determined that surveys would have to be repeated $\geq$4 times in order to have a 0.90 overall probability of detecting a Montezuma quail given the species is present. However, whether such sampling effort is logistically possible for an agency depends on the size of area to be surveyed and the time, personnel, and resource budget of the agency.

MANAGEMENT IMPLICATIONS

This study represents a first attempt to evaluate a monitoring technique for Montezuma quail in western Texas using presence–absence data obtained with call-back surveys. In general, this a presence–absence approach holds promise as a plausible and practical approach to monitor Montezuma quail in western Texas, particularly if a continued refinement of a probability of occupancy map occurs resulting from continued sampling of all vegetation communities. An improved probability of occupancy map would allow for efficient allocation of survey points and a more informed selection of a survey route.

Below we present a general survey protocol for Montezuma quail based on our findings. The protocol entails the following:

- *Establishment of survey points*. If monitoring is to occur within a specified, limited area and this area is reasonably accessible, then we recommend that an 800 $\times$ 800-m^2 grid be used to establish survey points because a grid of this size appears sufficient to minimize the probability of double counting given our experience. Alternatively, survey points may be established along a route with a spacing of $\geq$2 km and allocated in such a manner as to obtain a diverse representation of the different vegetation communities.
- *Conducting call-back surveys*. Call back surveys should be conducted during the breeding season, preferably to coincide during peak calling and the monsoon rains (e.g., Jun–Aug). Call-back surveys may be conducted either within the morning (0700–1100 hr) and/or evening hours (1500–1900 hr; Gonzalez 2012) and consist of playing the Montezuma quail call recording for approximately 1.5 minutes and then pausing to listen for a Montezuma quail response, repeating the process for 5 minutes. Each monitoring site will need to be visited $\geq$4 times during the field season.

Developing a practical monitoring approach for Montezuma quail will permit a better understanding of the species ecology. A presence–absence survey that provides occupancy estimates through time could be used to evaluate the influence of factors such as weather, habitat changes, land-use practices on the species. Furthermore, occupancy estimates would permit a better understanding of the species' conservation status and changes to its spatial distribution. Thus, a refinement of such a presence–absence survey through continued research is warranted for improved management and conservation of the species.

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CHANGES IN HABITAT USE OF MONTEZUMA QUAIL IN RESPONSE TO TREE CANOPY REDUCTION IN THE CAPITAN MOUNTAINS OF NEW MEXICO

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ABSTRACT

Montezuma quail (*Cyrtonyx montezumae*) are unique among quail with respect to clutch size, diet, covey dynamics, and habitat use. With the exception of a few notable early studies, there is relatively little information on the ecology of Montezuma quail. Pervious research has indicated that one of the primary habitats utilized by Montezuma quail is pinyon–juniper (*Pinus* spp.–*Juniperus* spp.) woodlands. Throughout many areas of the southwestern United States, pinyon–juniper woodlands are often targeted for thinning projects. Many studies have been conducted on the amount of canopy cover needed by other quail species. However, data on characteristics of their preferred habitat in many of the mountains they inhabit is limited in the literature and no data are currently published on their response to thinning projects. Therefore, studies are warranted to fill in these missing data, which will increase our knowledge about the habitat requirements of Montezuma quail and allow us to make informed decisions about thinning projects in areas occupied by Montezuma quail. The goal of this research was to evaluate Montezuma quail responses to common silvicultural practices, specifically pinyon–juniper thinning in the Capitan Mountains of New Mexico. Results of our project indicated that Montezuma quail selected for sites that had been thinned to reduce canopy cover to a 30–40% mosaic. Selection for this habitat was much higher than selection for the surrounding area, which consisted of $\geq$70% canopy cover (Manly–Chesson Selectivity Index = 1.68). Overall, this study yields vital information for managers considering implanting thinning projects in Montezuma quail habitat.

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Key words: canopy cover, *Cyrtonyx montezumae,* habitat management, Montezuma quail, population characteristics, thinning

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EFFECTS OF SOURCE POPULATION AND RELEASE STRATEGY ON SURVIVAL AND DISPERSAL OF TRANSLOCATED SCALED QUAIL IN THE ROLLING PLAINS OF TEXAS—A PRELIMINARY REPORT

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ABSTRACT

Scaled quail (*Callipepla squamata*) have declined 3.5% annually in Texas from 1966-2013, but declines have not been uniform across the state. The Rolling Plains Ecoregion has experienced a 6.8% decrease during this period, while the western Edwards Plateau has remained stable. Habitat loss that has contributed to scaled quail decline also inhibits recolonization. Translocation has become an increasingly popular tool to reestablish populations for recreational or conservational purposes. Overall success rate of translocations is low and has prompted research into factors that contribute to the establishment of a self-sustaining population. Source population and release strategy are two translocation tactics that may influence the success of scaled quail translocation efforts. Best practices for translocation are often species and location specific and, thus, it is critical for translocation techniques to be tested across a variety of species and landscapes. We used radio-tagged quail to estimate survival and dispersal of translocated, wild-caught scaled quail as a function of source ecoregion and a delayed release treatment using multi-state models in Program MARK. Specifically, we compared quail sourced from within the Rolling Plains and from the Edwards Plateau, as well as a delayed release treatment consisting of 4–8 week holding periods on site.

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Key words: *Callipepla squamata*, dispersal, reintroduction, scaled quail, survival, translocation.

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EFFICACY OF A SOFT RELEASE STRATEGY FOR TRANSLOCATING SCALED QUAIL IN THE ROLLING PLAINS OF TEXAS

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ABSTRACT

Scaled Quail (*Callipepla squamata*) populations have become locally extinct and spatially fragmented in the Rolling Plains ecoregion of Texas. Translocating Scaled Quail from core to declining populations could augment populations or re-establishing extinct populations. Although translocations of scaled quail have been attempted in Texas, none have been documented and none have attempted to identify best practices. Release strategy (i.e., hard or soft release) is a factor that can influence the success of a translocation. Our objective was to compare daily apparent survival of scaled quail translocated to the Rolling Plains between 2 release treatment groups: hard- and soft-release. We estimated a daily apparent survival rate (DASR) for radio-marked hens during the breeding season as a function of age, release treatment, and a time trend. We found evidence of a positive effect of the soft release treatment and higher DASR in adult hens. Overall, DASR of translocated hens was low compared to reported estimates of survival in established resident populations. Using a soft release strategy and translocating a greater proportion of adults may improve future translocation success for scaled quail.

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Key words: *Callipepla squamata*, dispersal, reintroduction, scaled quail, survival, translocation

INTRODUCTION

Scaled quail (*Callipepla squamata*) have declined by ∼ 7% per year since 1966 in the Central Mixed Grass Prairie (Sauer et al. 2014), an area that includes the Rolling Plains Ecoregion of Texas and Oklahoma (Gould 1975). Concurrently, scaled quail core distribution shifted to include only the westernmost portion of their historic range leaving small isolated populations where they were once abundant in the Rolling Plains Ecoregion of Texas and southwestern Oklahoma (Sauer et al. 2014, Rollins 2007, Silvy et al. 2007). Scaled quail in the Rolling Plains experienced an abrupt decline in 1988 and have remained at low abundance since (Rollins 1997, 2007). Although scaled quail are capable of dispersing long distances (up to 70 km) in wet years (Campbell and Harris 1965), habitat fragmentation in the Rolling Plains ecoregion as a

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result of human activities (Bridges et al. 2002, Rho 2015) and prolonged drought (Lusk et al. 2007, McGregor 2015) may restrict these movements preventing recolonization or augmentation of remnant populations. Additionally, the characteristic 2–3 year boom and bust cycles exhibited by scaled quail do not occur at low densities causing isolated populations to decline without an influx of new individuals (Lusk et al. 2007).

Considering these factors, translocation of scaled quail from source areas could reestablish or increase remnant populations (Armstrong and Seddon 2008, Griffith et al. 1989). Translocation has been well researched as a tool for restoring northern bobwhites (*Colinus virginanus*) with success documented in the southeastern United States (Terhune et al. 2006a,b; 2010). Translocation of bobwhites to the Rolling Plains ecoregion was successful based on short-term survival and dispersal, but population monitoring 2-years post-release did not demonstrate an increase (Downey 2015). Populations of scaled quail have been established successfully outside their native range in east-central Washington and eastern Nevada, although neither of these efforts were well documented (Schemnitz et al. 2009).

Release strategy, whether hard or soft release, can impact the success of a translocation and these impacts are often species specific (Batson et al. 2005, Moseby et al. 2014). In general, social species with small home ranges benefit from a soft release because of an increase in site fidelity due to reduced homing instincts (Moseby et al. 2014). Quail translocations have employed both hard (Terhune et al. 2005, Downey 2015) and soft release strategies (Stephenson et al. 2011, Scott et al. 2013), but no studies have directly compared release techniques. A translocation program with wild-trapped scaled quail using a soft-release technique was conducted at the Rolling Plains Quail Research Ranch, Fisher County, Texas, and has been effective, at least in the short-term (Pers. Comm. D. Rollins, Rolling Plains Quail Research Ranch).

The long-term goal of a translocation is to establish a self-sustaining population (Griffith et al. 1989). In the short-term that goal is dependent on the initial survival, dispersal, and reproduction of the founding individuals on the release site (Terhune 2010). Our objective was to compare apparent survival of translocated scaled quail between two release treatment groups, hard and 4-week soft release, to determine the effectiveness of either method to guide future releases. Additionally, we wanted to document maximum distance dispersed, nest initiation, and nest success of translocated scaled quail.

STUDY AREA

The release site was Matador Wildlife Management Area (WMA) in the central Rolling Plains ecoregion in Cottle County, Texas. Matador WMA is an 11,400-ha property owned and managed by Texas Parks and Wildlife Department. It was purchased in 1959 for the stated purposes of wildlife research, wildlife management, and public use. Public use activities include camping, hiking, fishing, and hunting of white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), feral hogs (*Sus scrofa*), Rio Grande turkey (*Meleagris gallopavo intermedia),* dove (*Zenaida* and *Streptopelia* spp.), and northern bobwhite.

Average rainfall and snowfall on Matador WMA are 56 cm and 7 cm, respectively. Soils are comprised predominantly of Woodward and Quinlan loams, Hilgrave sandy gravelly loam, Yomont fine sandy loam, Devol loamy fine sand, and Miles fine sandy loam (Natural Resource Conservation Service 2015). Terrain on the WMA is slightly sloping sandy upland with rough broken land in drainages. Mesquite (*Prosopis glandulosa*), sand shinnery oak (*Quercus havardii*), and sandsage (*Artemisia filifolia*) are dominant woody plants on coarse-textured soils whereas redberry juniper (*Juniperus pinchotii*) dominates on finer-textured soils and breaks. Grasses are primarily gramas (*Bouteloua* spp.), sand dropseed (*Sporobolus cryptandrus*), silver bluestem (*Bothriochloa saccharoides*), and threeawns (*Aristida* spp.)

METHODS

We captured scaled quail from 3 locations using walk-in funnel traps (Stoddard 1931) baited with sorghum and covered with natural vegetation to reduce stress and mortality of captured birds. Quail were captured on the 3 different source locations in Sterling and Bailey Counties, Texas during an 8-day period (17– 24 March) in 2015. Each quail was leg-banded, weighed, and classified by age and sex. We assumed that quail captured in the same trap were in the same covey and attempted to keep coveys together for release. Each covey group was then randomly assigned a release treatment (i.e., hard- or soft-release). The females were fitted with a 6-g necklace style radio transmitter (American Wildlife Enterprises, Monticello, FL). We chose to collar females only for two reasons: 1) we were interested in documenting reproduction, and 2) females would presumably pair with released males resulting in dependent survival and dispersal among pairs (reducing our sample size). All quail were transported to the release site within 24 hours using a plastic quail carrier (GQF Manufacturing Company Inc., Savannah, Georgia) covered with a black sheet to reduce stress. Quail assigned to a hard-release treatment were released immediately upon arriving on site. Soft-release birds were placed in one of 3 holding pens similar to the commercially available Surrogator® (Wildlife Management Technologies, Wichita, KS). Each holding pen housed 12–15 translocated quail. All holding pens were stocked with food, in the form of layer ration and sorghum, and water which was available to the quail ad libitum. All soft-release quail were held for 3–4 weeks and were then released on the same day (22 April 2015). All trapping, handling, and marking of scaled quail was done in accordance with protocols approved by Texas A&M AgriLife Research Animal Care and Use Committee (AUP # 2013-004A) and with permission from Texas Parks and Wildlife (Scientific Research Permit No. SPR-0690-152).

Radio-marked hens were monitored daily for 159 days during the breeding season from 18 March to 25 August 2015. We recorded survival (i.e., live or dead), location, nesting status (i.e., currently incubating or not nesting), and nest fate (i.e., hatched, or failed). Locations were obtained by homing in on the hen and semi-circling it. We attempted to locate missing quail by searching for them on county roads adjacent to the WMA. Once a bird was located, we continued daily monitoring. We additionally searched for missing quail by flying transects spaced 2-km apart with a 20-km buffer around the Matador WMA on 24 June 2015.

Although we attempted to locate hens daily, the rough terrain and long dispersal distances relative to the range of the collar (<1 km) resulted in uneven monitoring intervals for most individuals and probability of detection < 1. Therefore, we estimated daily apparent survival rate (DASR) for radio-marked hens using Cormack-Jolly-Seber (CJS) models rather than known-fate models in Program MARK. CJS models allow for the estimation of apparent survival (i.e., the probability that the individual survives and stays on the study site) and detection. For all models we allowed detection to vary between two groups: 1) hens that we were able to monitor consistently until death or to the end of the monitoring period (i.e., high detection), and 2) hens that went missing during the monitoring period (i.e., low detection). The models we developed included 3 variables to describe variation in DASR.

1. *Age*.–We included age at capture as a categorical predictor to describe variation in DASR between subadults (<1 year old quail, hatched in the preceding summer) and adults (>1 year old quail). Although age has been shown to influence survival in resident bobwhite quail, Terhune et al. (2010) found no effect for translocated bobwhites. Therefore, we hypothesized that we would also find no influence of age in translocated scaled quail, particularly because subadult quail at the time of capture would likely be >8 months old.
2. *Release method*.–We hypothesized that DASR would be greater for quail in the soft-release treatment based on the supposition that the holding period would allow quail to recover from the stress of capture and transport, avoid the peak of raptor migrations, as well as decrease homing instincts (Batson et al. 2015, Downey 2015).
3. *Time Trend*.–We included a linear time trend to describe an increase or decrease in DASR over the monitoring period. Our hypothesis was that DASR would increase over the monitoring period as quail became more familiar with their surroundings.

We assessed relative support for each model using Akaike's Information Criterion with a correction for a small sample size (AIC$_c$). Candidate models included all combinations of factors as well as the null and global models. Models <2 ΔAIC$_c$'s from the top model were considered competitive (Burnham and Anderson 2002). Within those competitive models, we evaluated the influence of each covariate using 80% confidence intervals of beta estimates (Arnold 2010). If the confidence interval overlapped zero we assumed the parameter was uninformative.

RESULTS

We trapped, banded, and translocated a total of 88 scaled quail to the Matador WMA during March 2015. This included 40 radio-marked hens, 47 males, and 1 unknown. Forty-two quail ($n = 17$ hens) were randomly assigned to a soft-release treatment and 46 ($n = 23$ hens) to a hard-release treatment. Overall, 73% ($n = 64$) quail were juveniles. Within the treatments, 81% ($n = 34$) and 65% ($n = 30$) of the soft- and hard-released quail, respectively, were juveniles. The discrepancy was due to variation in the number, age, and sex of quail captured on a particular day and our protocol to keep quail captured together in their covey units. Thirteen hens went missing permanently during the monitoring period: 3 (17%) soft and 10 (43%) hard released. We did not observe radio-marked hens coveyed with other hens after two days post release, therefore we assumed the fates of hens to be independent.

We observed the first hen nesting on 24 May 2015. At the time of nest initiation, 11 hens were missing from the study site (10 hard released) and 7 were observed dead (5 hard released). This made the effective sample size for nest initiation 8 and 14 hens for hard and soft release, respectively. We recorded 7 nests (1 hard released; 6 soft released); all were successful. The average clutch size was 12 eggs (range 8–15). Most nests were composed of multiple substrates. The most common nesting substrates were sand dropseed (N = 3) and prickly pear (N = 3, *Opuntia engelmannii*), but yucca (*Yucca* spp.), redberry juniper, broom snakeweed (*Gutierrezia sarothrae*), and plains bristlegrass (*Setaria vulpiseta*) were also used. Dispersal distances ranged from 0.5 to 22 km and averaged 6.7 km. Most hens (85%, $n = 34$) dispersed >2 km from their respective release point and 30% ($n = 12$) dispersed >10 km. The mean maximum distance dispersed by hard-released hens was 10.3 km (SD = 5.93) compared to 6.8 km (SD = 6.89) by soft-released hens.

Five models were within 2 ΔAICc of the top model and were considered competitive based on our *a priori* criteria (Table 1). These models included all three covariates describing DASR: age, release, and time trend. We interpreted 80% confidence intervals surrounding the beta estimate for each covariate from the model containing all three parameters. We found the confidence intervals for the covariate describing time trend to overlap zero indicating no measurable effect on DASR (Table 2). Covariates describing age and release showed a positive effect on DASR of soft over hard release and adult over juvenile hens, thus DASR of soft-released adult hens was highest ($\varphi = 0.99$, SE = 0.003) and DASR of hard released juvenile hens was lowest ($\varphi = 0.95$, SE = 0.01; Table 3). The estimated probability (P) of a soft-released adult versus juvenile hen surviving and not emigrating during the monitoring interval (159) was P = 0.33 and P = 0.08,

Table 1. Candidate model set describing apparent survival (φ) and detection (p) of translocated scaled quail at Matador Wildlife Management Area in the Rolling Plains Ecoregion of Texas during 2015. Covariates modeling apparent survival include age at capture (age), hard vs. soft release treatment (release), and a linear time trend (T). For all models we allowed detection to vary between two groups: 1) hens that we were able to monitor consistently until death or to the end of the monitoring period (i.e., high detection), and 2) hens that went missing during the monitoring period (i.e., low detection). Intercept only model included for comparison.

Model	AICc	Δ AICc	AICc Weight	k
φ (age + release), p (group)	1462.425	0	0.23089	5
φ (T), p (group)	1462.76	0.3411	0.19469	4
φ (release + T), p (group)	1462.84	0.4179	0.18735	5
φ (age + release + T) , p (group)	1463.04	0.6192	0.16941	6
φ (age + T), p (group)	1463.89	1.4711	0.11065	5
φ (release), p (group)	1464.04	1.6193	0.10275	4
φ (.), p (group)	1471.53	9.114	0.00242	3
φ (age), p (group)	1472.09	9.6691	0.00184	4
φ (.), p (.)	1507.85	45.425	0	2

respectively. Estimated probability of a hard-released adult versus juvenile hen surviving and not emigrating was $P = 0.03$ and $P < 0.01$, respectively.

DISCUSSION

Our data indicated a positive effect of the 4-week soft release treatment on DASR. No studies have directly compared release strategies when translocating quail, however several studies have employed a soft release technique in successful translocations of quails and other galliforms. Stephenson et al. (2011) held mountain quail (*Oreorytx pictus*) for 3-4 months prior to release and reported a successful translocation effort in terms of survival and reproduction. Scott et al. (2013) used a 7-day soft-release for northern bobwhites and reported no ill effects of the holding period. Rodgers (1992) documented a successful system for translocation of sharp-tailed grouse that involved holding wild-caught birds for up to 10 weeks prior to release. Many translocation efforts go unpublished. In an effort to capture this information, Snyder et al. (1999) used a questionnaire sent to wildlife biologists, managers, and researchers to report unpublished translocation attempts. They found that a soft release of prairie grouse species was positively correlated with translocation success.

In addition to the increase in DASR, the soft release technique also offers an advantage in terms of exposure to the environment (i.e. hens held in captivity are not subject to daily mortality). Scaled quail are most efficiently trapped from source populations before covey break-up which can occur as early as late-February. In our study, the first nest was detected in late May. Because we did not observe any mortality during the holding period for soft-release quail, this technique effectively protected translocated quail from natural mortality up to the time of release, roughly one month prior to nest initiation.

Although there was a positive effect of release treatment, the overall apparent survival of hens during breeding season in our study was low compared to other published survival rates of scaled quail. Rollins (2009) reported survival estimates of female scaled quail ranging from 0.67–0.80 and 0.22–0.48 in in Pecos and Brewster Counties, Texas (Trans Pecos ecoregion) and Sierra County, New Mexico, respectively. Survival documented by Pleasant et al. (2006) in Bailey County, Texas (High Plains Ecoregion) was 0.30–0.48. Both studies followed radio-marked female scaled quail during the breeding season from populations of resident, non-translocated birds. We would expect our estimates to be lower than true survival estimates (as apparent survival also includes the probability that the hen does not emigrate), however for 3 out of 4 groups apparent survival was <0.1.

Most hens dispersed >2 km from their respective release point. A distance that would exceed the typical home range size of 0.30–1.20 km^2 for scaled quail (Cantu et al. 2006). We observed 2 long distance movements of >20 km. These types of long distance dispersals have been documented in resident scaled quail populations, although they are thought to be infrequent (Campbell and

Table 2. Beta estimates and associated 80% confidence intervals (CIs) for juvenile vs. adult (age), hard vs. soft release treatment (release), and linear time trend (T) variables in models of apparent survival of translocated scaled quail at the Matador Wildlife Management Area in the Rolling Plains Ecoregion of Texas during 2015. For age and release the reference levels were juvenile and hard release, respectively.

Variables	Beta	SE	Lower CI	Upper CI
Release	0.81	0.48	0.20	1.43
Age	0.61	0.48	0.001	1.2
T	0.01	0.01	-0.01	0.02

Table 3. Estimates of daily apparent survival rates (DASR) and associated 95% confidence intervals (CIs) of scaled quail hens translocated using two release strategies. Hens were released at the Matador Wildlife Management Area in the Rolling Plains Ecoregion of Texas during 2015.

Release Strategey	Age	DASR	SE	Lower CI	Upper CI
Hard	Juvenile	0.95	0.01	0.92	0.97
	Adult	0.97	0.01	0.95	0.99
Soft	Juvenile	0.98	0.004	0.97	0.99
	Adult	0.99	0.003	0.98	0.99

Harris 1965, Cantu et al. 2006). It is important to note that one-third of the radio-collared hens went missing during our study period. Our probability of detecting radio-collared individuals was high on the WMA given our monitoring and search effort. Therefore, it is likely that these birds dispersed beyond our study area. As a result, the average dispersal distance for hard-release treatment is likely biased low because the missing hens were disproportionately from the hard-release treatment.

Our study is limited in scope and sample size, however it represents a novel attempt to assess the effects of differing release strategies and document a scaled quail translocation in the Rolling Plains ecoregion of Texas. We believe that future research efforts should attempt to document the short-term demographic parameters that we monitored at a minimum and potentially include males as well. If survival differs between sexes it may be advantageous for release groups to have a skewed sex ratio (in our study we attempted a to translocate males and females at 1:1). Long-term studies to document a population response pre- and post-translocation, as well as survival of first generation offspring, are immediate research needs. Future research should also address the appropriate scale at which to conduct and monitor scaled quail translocations. We intensively monitored 11,500 ha and aerially-searched approximately 125,000 additional ha, but were unable to locate all radio-collared hens throughout the monitoring period. This suggests that (a) our core study area may have been too small to effectively monitor survival and dispersal, and (b) more intensive monitoring may be necessary to keep up with dispersing scaled quail.

MANAGEMENT IMPLICATIONS

Based on the results of our study, it may be advantageous for future translocation efforts to use a soft-release technique and translocate a higher proportion of adults to maximize survival and minimize emigration off the release site.

ACKNOWLEDGMENTS

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SURVIVAL AND NESTING ECOLOGY OF SCALED QUAIL IN THE TRANS-PECOS, TEXAS

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ABSTRACT

Scaled quail (*Callipepla squamata*) are one of the most ecologically and economically important wildlife species in the Trans-Pecos, because they are the primary upland game bird in the Chihuahuan Desert. Using radiotelemetry, we evaluated survival (Kaplan–Meier) and nesting success of quail on 3 study sites in the Trans-Pecos, Texas: one (Santiago Mountain Ranch, central Brewster Co.) was supplemented with milo (*Sorghum bicolor*) year-round, the second (Lado Ranch, south Culberson Co.) never used supplements, and the third (Apache Ranch, central Culberson Co.) was supplemented with quail blocks. We trapped and radiocollared 164 female quail collectively across all study sites, and followed them for 2 years (May–Sep 2012–2013). There were no survival differences between years within study sites ($P = 0.985$), so we grouped data across years and compared survival between study sites. Apache Ranch had the lowest survival (55%) compared with the Santiago Mountain Ranch (76.3%) and Lado Ranch (75%). We found 47 nests across the reproductive seasons for 2012 and 2013. On average, scaled quail had high nesting success (72.6%), eggs per nest (11.6), and hatchability (91.25%). Nesting occurred from May to September with peak nesting in June and July. Timing and quantity of rain, combined with range conditions seemed to have the greatest effect on nesting performance.

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Key words: Callipepla squamata*,* nesting, scaled quail, survival

Scaled quail (*Callipepla squamata*) are a common quail species in the southwestern United States and northwestern states of Mexico (Johnsgard 1969). As a consequence of the decline of bobwhite (*Colinus virginianus*) across most of their natural range (Brennan 1991, 2002; Peterson et al. 2002), scaled quail could increase their importance as a game bird and provide an additional source of income for ranchers in the Chihuahuan Desert of Texas. However, since 1960 scaled quail have shown a 50% decrease in their populations over their entire range in the United States (Brennan 1993). The most common theories for their decline include predators (Rollins 2000), overgrazing (Bridges et al. 2002), drought (Wallmo and Uzzell 1958, Pleasant et al. 2006), disease (Rollins 2000), changing habitat conditions (Schemnitz 1994, Rollins 2000), reproductive failure (Pleasant 2003), or some combination of these factors (Bridges et al. 2001). Despite this, there has been little research done with respect to basic ecology of scaled quail.

Survival and cause-specific mortality of female quail has been studied in a number of locations and habitat types across much of their range (Rollins and Carroll 2001, Cox et al. 2004, Hernandez et al. 2006, Pleasant et al. 2006), but information is lacking in arid scrubland systems, particularly in the Trans-Pecos. Adult scaled quail survival can fluctuate widely by seasons; additionally, causes of mortality may also vary between seasons (Rollins and Carroll 2001). Several studies have observed seasonal variation in survival with the lowest survival occurring during periods associated with the reproductive season and nesting activity (Rollins 2000, Lerich 2002, Pleasant et al. 2006). Miller et al. (1998) suggested that incubation and brood-rearing activities may increase susceptibility to predation, leading to greater mortality during reproductive periods.

Scaled quail populations are believed to be maintained through high reproductive output in the form of large clutch size (Schemnitz 1994). Thus, reproductive

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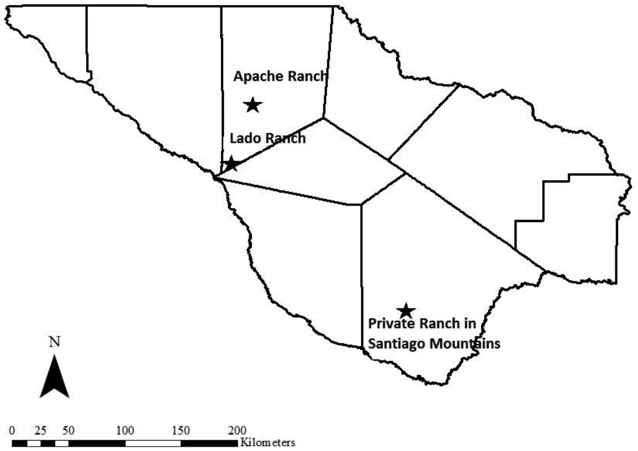

Fig. 1. Location of 3 ranches where scaled quail study sites were located in the Trans-Pecos, Texas, 2012–2013.

failure is likely to have a negative impact on population dynamics of scaled quail (Pleasant 2003). Predation has been documented to be the main cause of nest mortality (Martin 1993). Additionally, several studies have suggested there is a link between nest predation and precipitation (Palmer et al. 1993, Roberts et al. 1995). Although there is information available concerning the reproduction of scaled quail, most studies have been conducted prior to 1970 (Schemnitz 1994) and presents the disadvantage of having small sample sizes prior to the use of radiotelemetry (Schemnitz 1994, Rollins 2000). Thus, there is a great absence of knowledge on scaled quail nesting ecology (Pleasant 2003) and survival.

To approach the lack of knowledge, we initiated a study to better understand basic principles of reproduction, determine survival of female scaled quail, and identify causes of mortality that could allow land managers to promote suitable scaled quail populations.

STUDY AREA

We conducted the study on 3 different study sites, of which 2 provided supplemental feed. All 3 areas were in the Trans-Pecos region of Texas (Fig. 1). Santiago Mountain Ranch (Site 1; 11,300 ha) was located 104 km south of Alpine, in west-central Brewster County. Rainfall averaged 280 mm/year (NOAA 2012–2013) as compared with the Texas average of 700 mm/year. The elevation of the property at its highest point was 1,670 m above sea level. Ecological sites included Basalt Hill and Mountain Desert; Flagstone Hill; Gravelly; Gravelly, Desert Grassland; Gravelly, Hot Desert Shrub; Igneous Hill & Mountain, Desert Grassland; Igneous Hill & Mountain, Desert Grassland; Loamy and Desert Grassland (NRCS 2011). Typical plant species included junipers (*Juniperus* spp.), creosotebush (*Larrea tridentata*), lechuguilla (*Agave lecheguilla*), acacia (*Acacia* spp.), ocotillo (*Fouquieria splendens*), prickly pear (*Opuntia* spp.), and mariola (*Parthenium incanum*). Common grasses included black grama (*Bouteloua eriopoda*), blue grama (*Bouteloua gracilis*), chino grama (*Bouteloua ramosa*), and Lehmann lovegrass (*Eragrostis lehmanniana*). Most common forbs include common broomweed (*Xanthocephalum dracunculoides*), doveweed (*Croton* spp.), snakeweed (*Gutierrezia sarothrae*), and western ragweed (*Ambrosia cumanensis*). The study site contained supplemental feed with a feeder density of approximately 1 feeder/100 ha. Feeders were filled with sorghum and were available year-round. The ranch also had artificial water sources at a density of 1 waterer/200 ha.

The Lado Ranch (Site 2; 37,600 ha) was located 15 km south from Van Horn, in south Culberson County. The northern portion of the property consisted of desert flats transitioning to rolling hills with numerous draws. Southern portions included the Van Horn Mountains. Mean precipitation for the area was 305 mm with peak rainfall coming in August (NOAA 2012–2013). Ecological sites included Sandy Loam; Sandy Hills; Limestone Hill & Mountain; Loamy; Gravelly, Sandstone Hill & Mountain; and Igneous Hill & Mountain. Common shrub species included creosotebush, tarbush (*Flourensia cernua*), mariola, acacia, lecheguilla, prickly pear, ocotillo, sotol (*Dasylirion* spp.), and mesquite (*Prosopis* spp.). Primary grasses included blue grama, black grama, tobosa (*Pleuraphis mutica*), threeawns (*Aristida* spp.), tridens, and sacaton (*Sporobolus* spp.). Neither supplemental feed nor artificial water sites occurred on the Lado Ranch (Temple 2014).

The Apache Ranch (Site 3) was 50 km north east from Van Horn, in central Culberson County. Annual rainfall ranged from 280 to 380 mm (NOAA 2012–2013) across the study site with more precipitation occurring farther east and with increase in elevation across the study sites. Ecological sites included Gravelly, Limestone Hill and Mountains; Limestone Hill Dry Mixed Prairies; Loamy; Sandy Loam (NRCS 2011). Grass species include black grama, blue grama, sideoats grama (*Bouteloua curtipendula*), threeawn, tobosa, and alkali sacaton (*Sporobolus airoides;* Hatch 2007). Forbs, shrubs, and trees include fourwing saltbush (*Atriplex canescens*), creosotebush, tarbush, Apache plume (*Fallugia paradoxa*), skeleton-leaf goldeneye (*Viguiera stenoloba*), broom snakeweed, lecheguilla, ocotillo, yucca (*Yucca* spp.), and sotol were also found frequently throughout the study site (James 2013). Supplemental feed was provided as quail blocks on a year-round basis at a density of 1 block/150 ha. The ranch also had artificial water sources at a density of 1/240 ha.

METHODS

We captured scaled quail using funnel traps with chicken scratch (grained sorghum, corn, and sunflower seeds) or sorghum between September 2011 and August 2013. We set traps in Santiago Mountain Ranch and Apache Ranch near feeding areas while we set Lado Ranch traps near areas were quail were known to be. We aged quail based on wing molt and gender by presence (female) or absence (male) of brown streaking on their neck (Cain and Beasom 1983). We allocated mortality sensitive radiotransmitters (Model AWE-Q; American

Wildlife Enterprises, Monticello, FL, USA) for 2012 and Advanced Telemetry Systems transmitters for the year of 2013 (Advanced Telemetry Systems, Isanti, MN, USA). Once we recorded measurements, we released quail at the same location as capture.

We used a directional antenna (yagi) and receiver for tracking quail and used a Global Positioning System (GPS) unit to record quail locations approximately 2 times/week. We assumed independence of locations by acquiring only 1 location in each 24-hour period (Swihart and Slade 1985). We confirmed each quail location by visual observations. We calculated survival using Kaplan–Meier staggered-entry design equation (Pollock et al. 1989). We excluded from analysis individuals that died within 1 week of capture to remove any bias that may have been associated with capture myopathy. We censored individuals who experienced radio-failure or whose signal was lost over time. We captured all females during the spring and summer (15 March to 15 May); therefore, we did not segregate age classes because all individuals were either adults ($\geq$1 yr old) or subadults ($\leq$1 yr old) being recruited into the adult population. We used a single-factor analysis of variance to evaluate differences between sites. There was no difference in survival within sites ($P = 0.985$), so we grouped samples within sites.

When we detected a mortality signal, we made attempts to recover the quail as soon as possible to determine cause of death. We grouped mortalities into 4 categories: mammalian, avian, predation caused by unknown predators, or unknown. We classified scaled quail as being killed by mammalian predators if the carcass was cached, or if we found mammalian tracks or scat on or in close proximity to the kill site (Dumke and Pils 1973, Curtis et al. 1988). We classified quail as being depredated by avian predators if the radiotransmitter was located in a shrub or tree or if the radiotransmitter presented marks typical of avian predators. If predation was evident but no identifiable predator sign was found, we classified the bird as being killed by an unknown predator. We classified deaths as unknown when scavengers had destroyed the carcass before recovery, or if there was no obvious sign of predation or injury (Carter et al. 2002).

We did not experience problems with collars (American Wildlife Enterprises, Model AWE_QLL) in year 2012. However, approximately 50% of the collars allocated in 2013 (Advanced Telemetry Systems) malfunctioned; therefore, we had problems obtaining breeding season 2013. We also used the GPS units to mark nest locations. Once we located nests, we monitored them to assess fate (nest success, no. of eggs, eggs hatchability, and timing of incubation.). We grouped causes of nest predation into 4 categories (mesomammals, snake, predation caused by unknown predators, or nest abandonment) based on condition of the nest, egg shells, and visible sign in the immediate area. We classified nests as being depredated by mesomammals if the nest was destroyed or if eggs were fragmented and the nesting female was never seen with chicks after the event, or if we found mammalian tracks or scat on or near the nest site. If predation was evident by disturbance of nest and eggs, but no identifiable predator sign was found, we classified the nest as predated by an unknown predator (Staller et al. 2005). We considered nests to be abandoned if eggs remained intact, but incubation was not completed (Rader et al. 2007).

To classify nesting habitat, we used a 1-m^2 frame (Daubenmire 1959) to measure ground cover (relative percentages of bare ground, litter, succulents, grasses, forbs, and woody vegetation $<$2 m in ht and $>$2 m in ht). We divided specific cover percentage into categories as follows: 1 = 0–1%, 2 = 1.1–5%, 3 = 5.1–25%, 4 = 25.1–50%, 5 = 50.1–75%, and 6 = 75.1–100%. We also documented species composition in a 1-m^2 frame placed directly over the nest to determine primary nesting plant structure. Also, we estimated lateral visual obstruction using a Robel pole (Robel et al. 1970) placed at the nest center. We recorded the lowest reading at 10-cm intervals that were $\geq$50% visible in each of the 4 cardinal directions and calculated an average of the 4 readings to provide a single value for each nest site.

RESULTS

On Santiago Mountain Ranch in 2012, we trapped 153 scaled quail (60 M, 72 F, 21 unidentified gender). We radiocollard 17 females and obtained a survival estimate of 75% for the 2012 breeding season. In 2013, we trapped 129 quail (25 M, 62 F, 42 unidentified gender). We radiocollard 58 females and obtained a survival estimate of 70% for the 2013 breeding season.

On the Lado Ranch in 2012, we trapped 149 scaled quail (59 M, 55 F, 35 unidentified gender). We radiocollared 8 females and obtained a survival estimate of 78% for the 2012 breeding season. In 2013, we trapped 62 quail (32 M, 30 F). We radiocollared 30 females and obtained a survival estimate of 70% for the 2013 breeding season.

On Apache Ranch in 2012, we trapped 78 scaled quail (4 M, 19 F, 55 unidentified gender). We radiocollared 19 females and obtained a survival estimate of 47% for the 2012 breeding season. In 2013, we trapped 70 quail (32 F, 38 unidentified gender). We radiocollared 32 females and obtained a survival estimate of 54% for the 2013 breeding season.

Kaplan–Meier survival analysis showed a marked decrease in survival mainly in the months of April through July (Fig. 2). Primary causes of mortalities were raptors, mesomammals, and mortality due to human disturbance (Fig. 3).

We documented 47 total scaled quail nests in 2012 and 2013. We did not include Apache Ranch in analysis of nesting because of problematic data. Santiago Mountain Ranch nests ($n = 30$) had an average of 11.25 eggs/nest, 85% egg hatchability, and 71% nesting success. Five of the nests were predated by mesomammals. Two nests were abandoned, possibly because of inadvertent harassment of females caused by our telemetry efforts. Lado Ranch nests ($n = 17$) had an average of 11.5 eggs/nest, 97.5% hatchability, and 47% nesting success. Six of the nests were destroyed by predators and 2 nests were unsuccessful because the females were killed by predators.

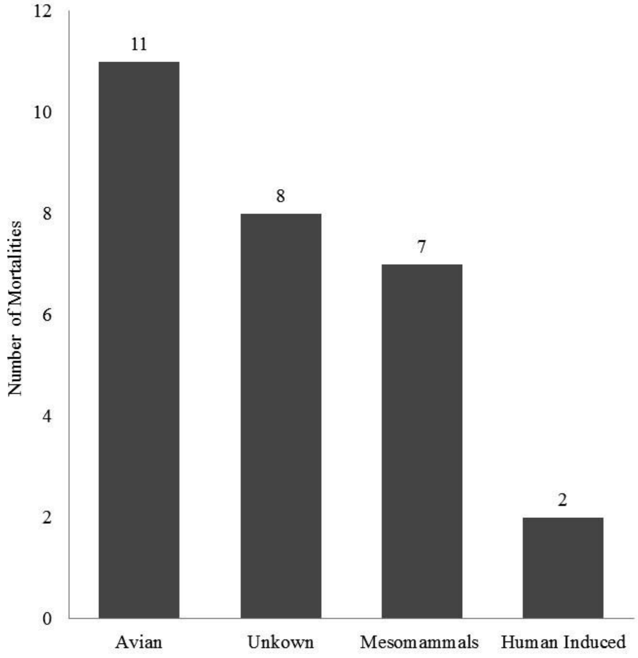

Fig. 2. Cause–specific mortality of scaled quail during reproductive season (Mar–Sep) on 3 restudy sites in the Trans-Pecos, Texas, 2012–2013.

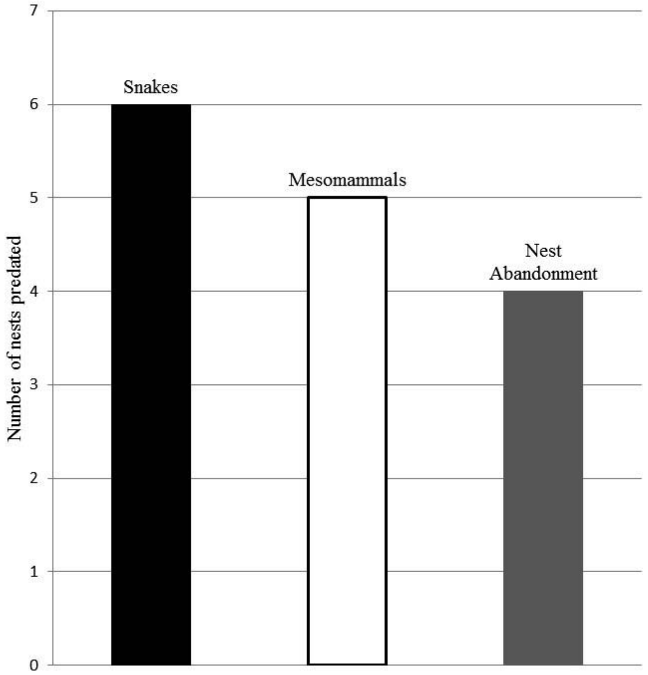

Fig. 4. Causes of failure for scaled quail nests during reproductive season on 3 study sites in the Trans-Pecos, Texas, 2012–2013.

Nest predation ($n = 15$) was mainly attributed to snakes ($n = 6$; 40%) because snakes predated 5 nests (only Lado Ranch; Fig. 4). Mesommals accounted for 33.3% ($n = 5$) of nest predations. Some females ($n = 4$; 8.5%) abandoned their nest, possibly because of disturbance induced by our telemetry efforts. We did not document predation from unknown cause in either study site.

Categorical values (1 = least amount to 5 = greatest amount) of vegetation on nest locations for both ranches averaged 3.3 for bare ground, 3.0 for litter, 2.3 for forbs, 3.6 for grasses, and 4.0 for succulents (Fig. 5). On Santiago Mountain Ranch, scaled quail selected a greater diversity of plants used for nesting. Quail on Lado Ranch seemed to have selected for sotol (33.76%) and lechuguilla (20.77%) (Fig. 6). Other plants used for nesting include ocotillo (6.49%), chino grama (6.49%), prickly pear (6.49%), Spanish dagger (*Yucca schidigera;* 5.19%), tasajillo (*Cylindropuntia leptocaulis;* 3.89%), whitethorn acacia (*Vachellia constricta;* 3.89%), tarbush (3.89%), sacahuista (*Nolina microcarpa;* 2.59%), creosotebush (2.59%), mesquite (2.59%), and javelina bush (*Condalia ericoides;* 1.29%). Nesting peaked in July and ranged from April to September for a few cases (Fig. 7). Timing of nesting did not vary across study sites and seemed to be triggered by initiation of rainfall.

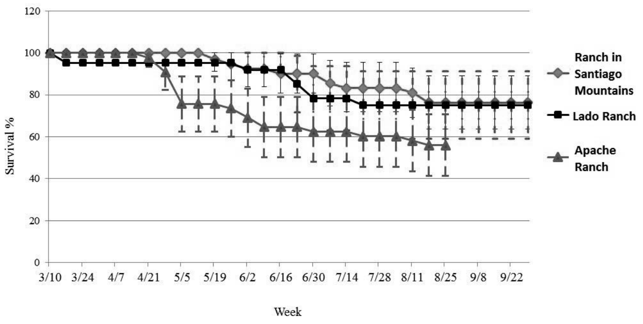

Fig. 3. Kaplan–Meier (Pollock et al. 1989) survival estimates and 95% confidence intervals for female scaled quail during 2012 and 2013 reproductive seasons combined at 3 study sites in the Trans-Pecos, Texas, 2012–2013. There was no significant year.

DISCUSSION

Compared with other studies (Rollins et al. 2006, Pleasant et al. 2006) we observed average to higher survival rates than have been reported in the past. There

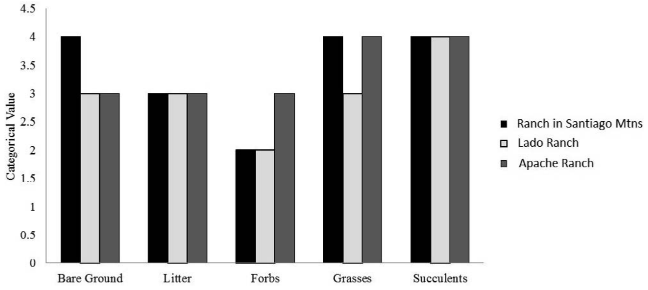

Fig. 5. Composition of vegetation present in each nest represented in categorical values (1 = least amount to 5 = greatest amount) for scaled quail nests found on 3 study sites in the Trans-Pecos, Texas, 2012–2013. Percent value for each category was grouped into categorical values for better interpretation because of lack of consistency when collecting data.

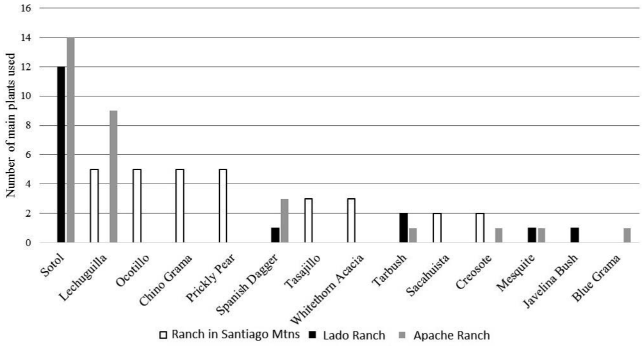

Fig. 6. Main plants used for nesting sites by scaled quail on 3 study sites in the Trans-Pecos, Texas, 2012–2013.

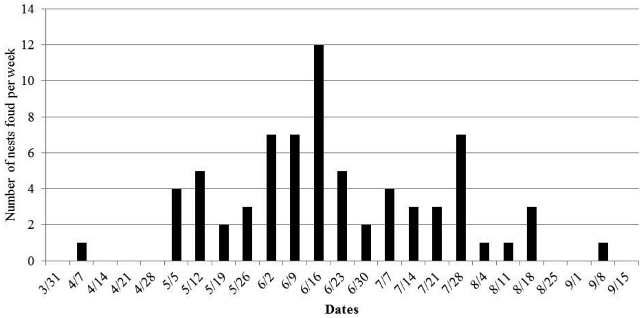

Fig. 7. Dates of nests found during scaled quail reproductive season on 3 study sites in the Trans-Pecos, Texas, 2012–2013.

was only a 1% difference in survival between Santiago Mountain Ranch and Lado Ranch. The greatest difference in survival was observed at Apache Ranch, with 19% lower survival than Lado Ranch and Santiago Mountain Ranch. Our research indicated that survival in Apache Ranch compares closely to the results from Pleasant et al. (2006), who reported survival of female scaled quail during the breeding season that ranged from 30% to 43%. Rollins (2000) estimated survival rates of female scaled quail to be 70%, which were similar to those we recorded at Santiago Mountain Ranch (76%) and Lado Ranch (75%). We noticed a decrease in survival beginning mid-April until mid-July, after which survival stabilized for all study sites. The decrease of survival may be due to a combination of factors such as avian predators, increased vulnerability of females on nests, and increased temperatures (21° C during spring to 35° C during the summer; NOAA 2012–2013).

During 2012 and 2013, we found the first nest in the first week of April and recorded the latest nest the first week of September. Brown (1989) observed that scaled quail would delay nesting season until summer rains in late June, July, or even August. Nesting season has been also acknowledged to last from April through September (Russell 1931, Bent 1932). The extended nesting season could increase the opportunity for successful nesting despite temporarily adverse weather conditions (Schemnitz 1961).

Literature reported highly variable nesting success for scaled quail; Leopold (1933) reported 8.3% and Schemnitz (1961) documented 14% success. However, these studies did not use telemetry equipment. Studies using radiotelemetry have shown consistently higher nesting success (36%, Lerich 2002; 44% and 64%, Pleasant 2003). These results are likely due to the difference in methodology and use of telemetry equipment as opposed to ecological differences. In this study, we documented high nest success ranging from 47% (Santiago Mountain Ranch) to 73% (Lado Ranch). Despite different reports on percentage of successful nesting (Russell 1931, Schemnitz 1961, Lerich 2002), hatching percentages seem not to vary between other studies and our results. Results from previous studies have reported 90% (Schemnitz 1968), 95% (Pleasant 2003), and 100% (Tharp 1971). In our study hatching rate was 85% (Santiago Mountain Ranch) and 97.4% (Lado Ranch), which falls between results from the previous mentioned studies. Predation seemed to be the most common cause of nest failure.

MANAGEMENT IMPLICATIONS

Weather conditions are believed to be a cause of short term and possibly long-term population trends of scaled quail (Schemnitz 1994). Studies support the theory that spring–summer rainfall is correlated with scaled quail population fluctuations (Wallmo and Uzzell 1958). The amount and timing of precipitation seems to have a pronounced influence on nesting success and annual population growth. Without optimum range conditions existing when rainfall occurs, maximum benefits for this species cannot be realized in terms of annual scaled quail numbers (Pleasant et al. 2006).

Differences in vegetation structure and composition may lead to greater survival of incubating and brooding females (Pleasant 2003). Heterogeneity of vegetation in an area may prevent predators from developing search patterns for grass-nesting birds (Martin 1988). A possible way to decrease loss of scaled quail populations is to increase cover and adequate loafing habitat (Rollins et al. 2006). This makes it a challenge to manage adequate vegetation structure, plant species composition, and arrangement of these plant communities because they may have a profound effect on survival of scaled quail populations (Pleasant et al. 2006).

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CONSERVATION STATUS OF THE MASKED BOBWHITE IN SONORA, MEXICO

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ABSTRACT

The historical distribution of the endangered masked bobwhite (*Colinus virginianus ridgwayi*) ranged from southern Arizona, United States, to Central Sonora, Mexico. Research in Sonora the past 30 years focused on the largest known populations, near the town of Benjamin Hill on the El Carrizo ranch. Research and perceptions by local residents pointed to a decline in masked bobwhite over the past decade. We evaluated existence of the subspecies during 2013-15 by searching transects and interviewing local residents. Our evaluation yielded no validated observations of masked bobwhite, and subsequently we call for further coordinated population monitoring and the development of technology to identify vocalizations by the subspecies.

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Key words: conservation status, endangered species, *Colinus virginianus ridgwayi*, masked bobwhite, México, Sonora

INTRODUCTION

Of 21 bobwhite subspecies currently recognized (Roskov et al. 2016), the masked bobwhite (*Colinus virginianus ridgwayi*) is the only subspecies included at the Convention on International Trade in Endangered Species of Flora and Fauna in the Appendix I category (CITES 2008). The masked bobwhite has been classified since 1994 by Mexican law (Norma Oficial Mexicana NOM-ECOL-059) as endangered (*en peligro de extinción*) (Diario Oficial de la Federación 2002), and it is a priority species in the Endangered Species Conservation Program of the Natural Protected Areas Commission (CONABIO 2011). Masked bobwhite distribution has shrunk from historic areas in the Altar Valley in southern Arizona, United States, and Central Sonora, Mexico, near Opodepe, Carbó, Trincheras, Magdalena and Benjamín Hill, (Garza-Salazar et al. 1992, Del Coro y Ceballos 2000), to a single wild population in Central Sonora. Population estimates for Central Sonora include 1,000 individuals during 1968-1972 (Tomlinson 1972), 1,000–2,000 early in the 21st Century (Hernández et al. 2006), and zero detected in 2010 (Gómez-Limón 2010, Convention on International Trade in Endangered Species of Wild Fauna and Flora. 2011). Because of the extremely low population estimates, Recovery Actions 3.11 and 3.12 of the U.S. Fish and Wildlife Service Masked Bobwhite Recovery Plan emphasized the need to determine if populations occur outside of the current survey areas in Central Sonora (U.S. Fish and Wildlife Service Buenos Aires National Wildlife Refuge 2014).

STUDY AREA

The study area included three ranches near the town of Benjamín Hill, in the state of Sonora, Mexico. The ranches were El Carrizo (40,500 Ha; Universal Transverse Mercator, UTM: 477865.00 m E, 3323932.00 m N, 722 meters above sea level), San Dario (UTM: 476757.00 m E, 3326795.00 m N, 727 meters above sea level) and El Seri (UTM: 475882.00 m E, 3316974.00 m N, 743 meters above sea level) (Figure 1). Rancho Hunting, a part of El Seri, included facilities to accommodate hunters that visited the ranch. The study was authorized by the landowners, Mr. Gustavo and Mr. Alejandro Camou, and conducted in coordination with the Alianza Mexicana para la Conservación de la Vida Silvestre (AMECVIS).

METHODS

We studied masked bobwhite using transects to detect birds during July–September, 2013, and March–May,

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Fig. 1. Map of the region of Mexico where study area is located. The study area included 3 ranches near the town of Benjamín Hill, in the state of Sonora, Mexico.

2014, followed by interviews of local residents, and subsequently, further searching in 2015 to determine potential existence of the species.

We surveyed in areas where masked bobwhite had historically occurred (e.g., the source of bobwhites translocated to Buenos Aires National Wildlife Refuge in 1999; Hernandez et al. 2006), as well areas where vegetation had been managed for wildlife (Martín-Rivera et al. 2001). We added another search location on the San Dario ranch based on information from Alejandro Quijada Sabori (reported in Results section), a ranch worker with 50 years of local experience. We created a reference point (UTM: 476999.00 m E, 3326611.00 m N. 721 meters above sea level) and searched within a 5-km radius.

Observers traversed transects, each 1.5 to 2.5 km long, searching an area about 2-3 m wide, listening for vocalizations and searching for sign and individuals. Observers were instructed to walk and stop for ten minutes at the beginning and end of each transect. Transects were randomly selected, with the exception of a path that followed the bed of streams. According to residents of the ranch they had detections anecdotal and historical (for several years) in sites located in this area. We sampled during diurnal periods when breeding masked bobwhite typically vocalize, 0600-0900 hours and 1800-2000 hours. We recorded vocalizations and submitted these data to the Macaulay Library Cornell Lab of Ornithology. Four observer groups, 2-4 individuals each, traversed an average of five transects per day and about 20 transects per week. Observers were ecology students from the Universidad Estatal de Sonora that we trained to identify the masked bobwhite based on photos, field sign, vocalizations, etc.

RESULTS

Total transect length was 225 km. Observers had a preliminary finding of masked bobwhite eggshell fragments, but did not retain a sample for definitive laboratory identification. Observers had a preliminary finding of a masked bobwhite vocalization, but upon further review, we rejected this identification. Thus, our observations along transects produced no evidence of the existence of masked bobwhite.

Follow-up anecdotal reports by local residents included: 1) visual observation in June 2014 of a single male masked bobwhite in a covey of Gambel's quail (*Callipepla gambelii)* adjacent to San Daria ranch by Ing. Marco Antonio López Figueroa; 2) a second-hand auditory observation in August 2015 of a female masked bobwhite on San Dario ranch by Mr. Alejandro Quijada Sabori. This was the basis for our search beyond the transect study, and subsequently we recorded a possible vocalization by a masked bobwhite on September 20, 2015, 0913 hours (UTM: 477294.00 m E, 3324346.00 m N. 717 meters above sea level). However, an enhanced version of the sound recording (Cornell Macaulay Library) was perceived to be a vocalization by a yellow-breasted chat (*Icteria virens*) by specialists of the Buenos Aires Natural Wildlife Refuge Masked Bobwhite Recovery Team.

DISCUSSION

Our finding of few, if any, masked bobwhite agreed with recent research and the perception of local residents that the subspecies population had declined since 2000. Our inability to validate a recording of what was perceived to be vocalization by masked bobwhite points to the need for development of a sonogram for the subspecies. We recommend continued searching on the El Carrizo ranch, and the development of coordinated research.

ACKNOWLEDGMENTS

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THE SAGA OF THE MASKED BOBWHITE: LESSONS LEARNED AND UNLEARNED

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ABSTRACT

No bird has generated so much interest and controversy as has the masked bobwhite (*Colinus virginianus ridgwayi*). From its discovery in 1884 to the present, this gallinaceous game bird has captured the attention of hunter-naturalists, ornithologists, collectors, game breeders, conservationists and bureaucrats. Believed threatened with extinction throughout its 130 year history, the masked bobwhite prompted several collecting expeditions, a survey technique study, a plethora of propagation attempts, and the purchase of an 117,464 acre refuge by the federal government, and expenditures totaling millions of dollars. Yet, despite propagated stock existing in a captive facility on Buenos Aires National Wildlife Refuge, the status of the masked bobwhite is now more perilous than ever, and this subtropical race of America's most popular game bird may now be functionally extinct. How this all came about is a lesson that needed to be learned by wildlife managers seeking to increase and secure wild populations of native game birds.

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Key words: Buenos Aires National Wildlife Refuge, Arizona, *Colinus virginianus ridgwayi,* masked bobwhite, propagation, Sonora, Rancho Carrizo, restoration

INTRODUCTION

The story of Herbert Brown's discovery of the masked bobwhite in Arizona and subsequent attempts to prevent the bird's extinction has been told several times (Tomlinson 1972a, Brown and Ellis 1977, Kuvlesky and Dobrott 1995, and most recently, Hernández et al. 2006, and Brown et al. 2012). Only 13 native masked bobwhite from five general locations in Arizona are in collections, all through Herbert Brown's efforts (Brown et al. 2012). By 1900, bobwhite could no longer be found in Arizona and the bird had disappeared before any attempt could be made to obtain aviary specimens or protect any of the wild bird's natural habitat (Brown 1900, Brown 1904, Breninger 1904).

After 1904, ornithologists concentrated on collecting masked bobwhite in Sonora, Mexico, where Frank Stephens had collected the original type specimen in 1884. Collectors such as J. C. Calhoon, and W. W. Brown scoured Sonora's *llanos* and *bajios*, not only to collect specimens, but also to describe the bird's habitat, and report on its distribution and abundance. Such activities were greatly curtailed, however, with the onset of the Mexican Revolution in 1910 and the Yaqui wars that followed through the 1920s. For some reason none of the expeditions seeking bobwhite extended southward into Sinaloa, and as far as is known, this race of bobwhite is very isolated (Aldrich and Duval 1954).

With the slacking off of hostilities in the late 1920s, J. T. Wright (1932:73-77) resumed the search for the masked bobwhite in Sonora, not only collecting specimens, but reporting on the bird's presence and abundance while his wife, Dora, mapped its distribution. In July 1931, he found masked bobwhite near Noria on Mexico's Southern Pacific railroad. Later, in October 1931 and March 1932, he found good numbers of bobwhite near San Marcial where he provided definitive habitat descriptions and important life history information. The Wrights' report led to the first attempts to capture masked bobwhite with the intent of restoring the species to the U. S. Unfortunately, the numerous attempts to reintroduce masked bobwhite to Arizona that followed have failed, and wild populations in Sonora may now be extinct. The history of these attempts and a discussion of the reasons for their failure to maintain sustainable wild population is the purpose of this report.

METHODS

We reviewed all of the published literature that was available and as many unpublished reports as we could locate to obtain as much information as possible on former masked bobwhite restoration attempts. That the senior author was professionally involved with this bird from 1964 through 1985, and knew many of the principals

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Fig. 1. Masked bobwhite specimen #78 acquired from an aviary by C. T. Vorhies in 1936. This adult male is thought to have been obtained from the La Cavernas restaurant in Nogales, Sonora, where it reportedly died from old age.

involved, was a major source of information on the early history of restoration attempts. Learning the birds' recent history was greatly facilitated by the second author being a member of the Masked Bobwhite Recovery Team with access to the team's files at Buenos Aires National Wildlife Refuge near Sasabe, Arizona.

RESULTS

Restoration Attempts, 1937–1967

The man who was to dedicate the most time and effort to restore masked bobwhite to the United States was J. Stokley Ligon, who showed an interest in this bird as early as 1913 while collecting birds in New Mexico for E. W. Nelson (Shaw 2011). With the improvement of conditions in Sonora in the late 1920s, interest in the bird revived and several ornithologists from California launched an expedition to obtain aviary stock near Magdalena, Sonora (Sheffler 1931). In 1927, noted oölogists Griffing and Margaret Bancroft stopped at a restaurant near Magdalena, where they ordered quail from the menu. On being informed that they would have to wait while the birds were killed and dressed, they asked to see the pens where the birds were kept. To the Bancroft's surprise, the quail within the wire mesh were masked bobwhite. Forgoing dinner, the Bancrofts purchased the live birds for their aviary in Tucson (Walker 1962-63). These quail (and supposedly their eggs) eventually found their way into museums, the final specimen (UAz001350) thought to have been deposited by C. T. Vorhies in the University of Arizona Bird Collection on 15 January 1936 (UAz001350, Figure 1; Brown et al. 2012). This intense subsistence trapping is a heretofore-unreported cause of the masked bobwhite's disappearance similar to that experienced by the imperial woodpecker (*Campephilus imperialis*) (Brown and Clark 2009). No attempt had been made to re-establish this masked bobwhite in Arizona or Mexico.

J.T. Wright had better luck, collecting 44 masked bobwhite between March 1929 and March 1932 in locations from Noria southeastward to vicinities near San Marcial and Tecoripa. Although no live birds were captured for propagation purposes, Wright's habitat descriptions, life history notes, and maps greatly aided further searchers such as Ligon.

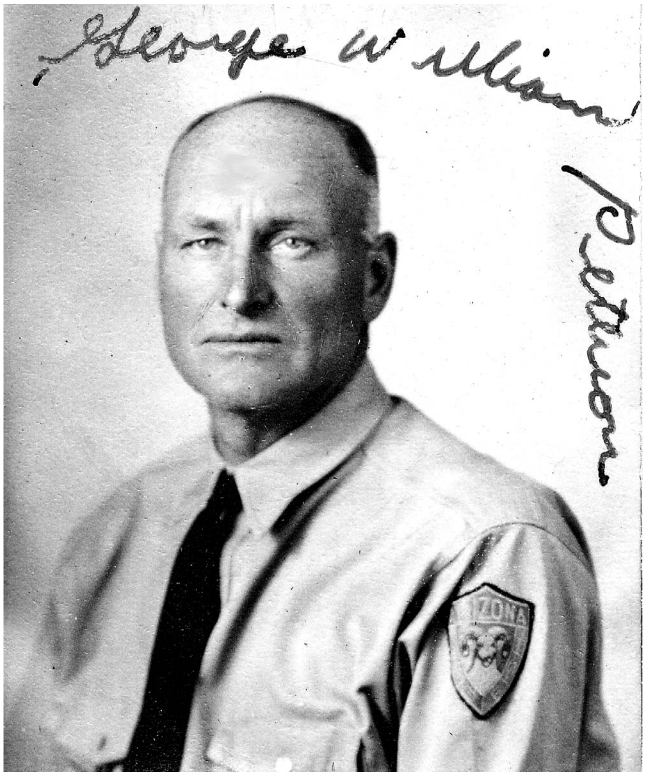

Fig. 2. Game Warden and ex-border patrolmen "Pete" Peterson. It was Peterson's fluency in Spanish and interest in masked bobwhite that resulted in masked bobwhite being located in several relict areas in Sonora.

In 1937, Ligon undertook the first of three expeditions to Sonora to obtain wild birds for release and propagation (Tomlinson 1972a). The first trip in December 1937 was made with David M. Gorsuch (1934), who had recently published a monograph on Gambel's quail. This trip resulted in the netting of >100 masked bobwhite in the Tecoripa and San Marcial areas. Other sites investigated included east of La Colorada, near Mazatán, and Laguna Larga (Ligon 1942, 1952).

Thirty-three of these wild-trapped birds were released in the San Rafael Valley and at the Nogales Ranger Station; the remaining birds were held for propagation at Ligon's game farm near Carlsbad, New Mexico. Most of the releases were in temperate short-grass habitats above or at the upper altitudinal limits of the masked bobwhite's historic range as a survey by Arizona Game and Fish Department Federal-Aid biologist O.N. Arrington (1942) found no suitable habitat remained within the bird's historic habitat in Altar Valley. Nor were any of the release sites dedicated to the recovery of masked bobwhite and no advance preparation was made for the bird's survival (Ligon 1942, 1952). Although 10 captive wild birds released at Jalisco Well near Arivaca initially showed promise (Arrington 1943), all of the releases eventually failed (Lawson 1951).

A second trip to obtain brood stock was taken in 1949 with Louis (Buzz) Lawson, the AGFD's Federal-Aid biologist in charge of small game investigations and the Arizona Game and Fish Commission's Game Ranger George Peterson (Figure 2). Despite spending almost a month during November and December in south-central Sonora, and revisiting the sites visited by Ligon in 1937, no birds were found. Ranchmen, who had formerly known of the presence of masked bobwhite, stated that the birds appeared to have vanished overnight. Ligon and the other investigators knew, however, that the reason for the birds' disappearance was livestock grazing during drought years (Lawson 1951). All indications were that masked bobwhite could not tolerate even moderate grazing of their tropical grassland habitats.

Not willing to give up, Ligon, Lawson and Peterson determined to make a third attempt at finding brood stock as rumors of masked bobwhite in Sonora persisted. After an extensive search in the same general areas for bobwhite feathers in cactus wren (*Camplorhynchus brunneicapillus*) and verdin (*Auriparus flaviceps*) nests in November 1950 a small covey of bobwhite was found near Tecolote Peak 60 miles east of Hermosillo. Then, after a long, difficult trip of > 100 miles, four coveys were located in tall grass near Punta de Agua in southern Sonora. Overall, 25 bobwhite were captured. Lacking proper habitat, but realizing that wild birds were inherently superior to propagated birds, 15 birds were released that year outside the bird's range in southwestern New Mexico and in Garden Canyon on Fort Huachuca. These releases also failed—a situation Ligon and AGFD Research biologist Steve Gallizioli attributed to the bird's being released in unsuitable non-historic habitat, the Garden Canyon birds not being seen >2 months after release. Ligon retained ten birds for propagation (Lawson 1951).

In 1961, the Arizona-Sonora Desert Museum began a study of pen-reared masked bobwhite using 30 propagated birds obtained from Ligon (Walker 1962-63). Knowing that the birds had been in captivity for >20 years and believing that breeding stock might never again be available, Lewis Wayne Walker and Ligon determined that a "do or die" effort must be done as carefully as possible.

After receiving a letter of support from Richard M. Scaife, Chairman of the Board of the Allegheny Foundation, Walker set about coordinating a recovery plan with Arizona Game and Fish Department Director Robert Smith, Arizona Bureau of Land Management Director Fred Weiler, and Arizona-Sonora Desert Museum Director William H. Woodin. Local ranchers were consulted and a revegetation plan pioneered by John Donaldson in which check-dams were used as water retention barriers agreed upon (Walker 1962-63).

After considering 10 different sections of valley land thought to be within the historic range of masked bobwhite, 259 ha of Bureau of Land Management land in Avra Valley were selected, seeded with grasses supplied by the Soil Conservation Service, and dedicated for masked bobwhite restoration. A well was drilled to irrigate the grasses during times of drought and 64 check dams constructed with bull-dozers. On the advice of quail breeders, holding cages of ca 0.5 ha were divided into 16 equal parts 7.6 × 30m. To provide an area for the birds to exercise but not escape, some 372 m^2 of roof wire,

Fig. 3. Masked bobwhite release site pens and enclosure as they appeared on completion in 1961. Emphasis was entirely on the reseeded grasses with no consideration apparently given to the provision of natural foods.

weighing 4535 kg covered the cages (Figure 3). The total cost was $15,000 – a sizeable sum for a volunteer organization headquartered in Pennsylvania.

Getting the birds to breed proved a problem as the birds showed little inclination to pair off. Round-tailed ground squirrels (*Citellus tereticaudus*) and kangaroo rats (*Dipodomys* sp.) ate the grass seeds and newly sprouting grasses outside the enclosure. Then disaster struck with the *chubasco* of September 26, 1962. Almost 18 cm of rain fell in 12 hours and visits to the site became impossible.

Fortunately, the cages had been placed on a sandy ridge, and by being on this island, some birds at least, weathered the storm. The source of consternation now was an eruption of black and yellow caterpillars, an infestation so great that chemical applications were considered as a means of control. Not being quail biologists, the Desert Museum caretakers were surprised and delighted when a delayed inspection trip showed two bobwhite fighting over a caterpillar. Later observations that day resulted in hearing at least 2 calling males and finding the remains of two eggs. The damage had been done, however. The check dams had been virtually eliminated and the remaining birds were now fewer in number. How many remained was problematical.

Located in an area dominated by creosote (*Larrea tridentata*), the release site was too dry to support a grassland and was probably outside the bird's historic range. The project was terminated in 1964 when the few birds remaining in the pen were either eaten or released by two boys from the nearby O'odham Nation. (Brown 1989). The remaining birds were sent to the University of California at Davis in an attempt to discover the reasons for the bird's poor reproductive performance (Tomlinson 1972a). No feral masked bobwhite have been documented from Avra Valley.

At about the same time Jim and Seymour Levy, two Tucson conservation-minded ornithologists, took up the masked bobwhite cause, searching for bobwhite in Sonora and raising propagated stock donated by Ligon, who was now >70 years old. Although hatching the eggs of captive birds proved difficult, their search for masked bobwhite in Sonora with AGFD Research biologist, Steve Gallizioli, succeeded beyond all expectations. In June 1964, while looking for elegant quail (*Callipepla douglasii*) on a ranch in Sonora 26 km south of Benjamin Hill, they saw and heard three coveys totaling *ca*. 20 masked bobwhite (Gallizioli et al. 1967). This ranch, also known as Rancho El Carrizo, differed from former masked bobwhite habitat descriptions in that tall grasses were generally lacking even though the area possessed an abundance of tropical grasses protected from grazing by dense stands of cholla (*Cylindropuntia fulgida*). Although the initial discovery only regarded 120 ha as occupied by bobwhite, later investigations showed some 65 km^2 to be bobwhite

Fig. 4. The senior author evaluating potential masked bobwhite habitat on Buenos Aires Ranch in 1969 prior to its acquisition as a National Wildlife Refuge. Note the tall grasses (*Sporobolus*) then present.

habitat. These were the first wild bobwhite seen by ornithologists in 14 years.

Realizing that the U. S. Bureau of Sport Fisheries and Wildlife was better equipped to raise masked bobwhite, the Levy's donated their four pairs of birds to that agency in 1965. However, after a year of moderate reproductive success at the Patuxent Wildlife Research Center at Laurel, Maryland, both egg production and fertility declined considerably. Patuxent personnel believed that the problem was due to inbreeding depression as the birds had been in captivity for 18 years. (Tomlinson 1972a).

In 1966, the masked bobwhite was included as a species protected by the U. S. Fish and Wildlife Service under the Endangered Species Act. Now that funding was available, the first priority was to see if some sort of arrangement could be made with Sr. Pedro Camou, the owner of Rancho Carrizo, to protect the masked bobwhite's habitat. Initial discussions with Sr. Camou and Mexican officials to set aside or purchase portions of Rancho Carrizo for masked bobwhite preservation were encouraging. Then, for reasons never fully explained, a management agreement to leave some pastures on Rancho El Carrizo ungrazed fell through. Rancho El Carrizo was divided among several owners and Sr. Camou only agreed to a grazing management plan that would include livestock as well as masked bobwhite on his 1,600 ha ranch (Tomlinson 1972b). Meanwhile, suggestions to purchase an adjacent or other suitable ranch as a masked bobwhite refuge went largely unexplored (Tomlinson 2006a).

Roy Tomlinson was assigned to study the masked bobwhite in 1967. Stationed in Tucson, Tomlinson was an excellent choice having worked as a state and federal biologist on mourning doves and other small game birds. His study began by researching a compendium of all that was known about the "species," searching for additional populations in Sonora, and conducting field studies into the masked bobwhite's life history on Rancho Carrizo. In addition to further investigations into the bird's habitat requirements, these studies included a call-count survey regimen that proved an excellent survey method to monitor masked bobwhite population abundance and declines. Tomlinson's discovery of a second population of masked bobwhite near Mazatán came to naught when the population died out during a drought.

Early Releases and Restoration Attempts

Nearly 60 wild birds were obtained by Tomlinson from Rancho Carrizo during population highs in 1968 and 1969 and shipped via quarantine to the Service's breeding facilities at Patuxent, MD. These birds produced more eggs and chicks than previous attempts, and provided a steady supply of birds for release (Tomlinson and Brown 1970). It was also in 1969 that the U. S. Fish and Wildlife Service, in cooperation with the AGFD, began searching for suitable reintroduction sites in Arizona. Four areas in and near Altar Valley were selected in 1970, none of them ideal. The Arizona sites were higher in elevation (730 to 1310 m) than the bird's Sonoran habitats (290-825 m) and lacked tropical diversity. All of the selected sites were generally rockier and lacked tall, tropical grasses. The Arizona sites were also subject to livestock grazing and the dense cover preferred by bobwhite elsewhere was limited (Tomlinson and Brown 1970; Figure 4).

In an attempt to reduce over-wintering mortality and provide nesting cover, the U. S. Fish and Wildlife Service leased 745 ha of the Las Delicias Ranch in Altar Valley from the Arizona State Land Department as a masked bobwhite release area in 1972. This lease, along with a Bureau of Land Management section on Rancho Seco between the Las Guias Mountains and Cerro Colorado were to provide nesting habitat free from grazing. However, when post-release investigation showed released birds preferred bottomlands (Brown and Ellis 1977), 465 ha of bottomland habitat on the Buenos Aires ranch in Altar Valley were leased from the Victorio Land and Cattle Company and the Las Delicias and Cerro Colorado leases were abandoned.

The first masked bobwhite from Patuxent—all pen-reared birds – had been released into the wild in 1970. Many of these birds suffered deformities due to excessive de beaking and confined rearing. After 1971, the quail were held in Tucson for three months prior to release, but it was not until 1974 that captive birds were released with any conditioning to the wild. Most of the birds disappeared within 2 months and mortality from predation was abnormally high (Ellis and Serafin 1977). By 1978, >7000 domesticated bobwhite had been released in Arizona. Dave Ellis, a raptor biologist assigned to the project to replace the retiring Roy Tomlinson, addressed the poor condition of the birds by experimenting with several innovative conditioning techniques.

In 1974, two conditioning techniques were initiated to produce more release-worthy stock (Ellis et al. 1978). One was a modification of the foster parent –adoption methods originally described by Stoddard (1931) and Hart (1933), and later modified by Stanford (1952). The most promising foster parents proved to be wild-caught Texas bobwhite (*C. v. taylori*) males sterilized by bilateral vasectomy (Ellis and Carpenter 1981). These male birds readily adopted masked bobwhite chicks, after which both were released on the study sites. The second technique was a modification of the call-box conditioning program proposed by Hardy and McConnell (1967:29) in which released birds are called back to a predator proof pen each evening by a calling female.

These techniques were tested with thousands of released masked bobwhite between 1974 and 1979 (Brown and Ellis 1984). With both pre-release and post-release training programs in place, propagated birds were thought to be more prepared for survival in the wild. Many of the birds released in 1976 survived into the winter, and by the onset of next year's summer rains ~30 masked bobwhite remained near their release sites on the Buenos Aires ranch. The following October a pair of masked bobwhite was sighted with at least three chicks—the first documentation of over-winter survival and recruitment by propagated stock. These birds were not far removed from their wild-trapped origins, and call-count surveys in 1979 resulted in 74 calling males being recorded – an all-time record of birds present.

In 1977, the first recovery plan was drafted, approved and published. In addition to continuing the propagation techniques already developed, an emphasis was placed on studying and transplanting wild stock when sufficient birds were available (Brown and Ellis 1977). Periodic burning and food plots were recommended to improve habitat quality and reduce the mortality of released pen-reared birds, which were exhibiting high mortality during the winter months. These birds were only a generation or two removed. In the meantime, quantitative studies by Goodwin and Hungerford (1977), Reichenbacher and Mills (1984), and Simms (1989) determined that the preferred habitats of released quails consisted of bottom lands containing 10-15% woody plants, 12 to 50% grass cover, and 10 to 15% forbs.

The Nature Conservancy negotiated a contract for managing the Sonoran habitats and for conducting field studies of the Sonoran investigations that left the management of Rancho Carrizo to an agreed upon livestock grazing plan. Setting up a burning regimen proved difficult on both sides of the border, and no attempt was made to improve the quality of birds being released in Sonora. Quantity was considered more than quality and the impact of these releases on wild birds went undocumented.

By 1979 a sizeable wild population of masked bobwhite was thought to be present on the Buenos Aires Ranch; the number of calling males had increased from 21 in 1977 to 74 in 1979 (Goodwin and Hungerford 1981). Thereafter, however, livestock grazing on the leased pastures, combined with summer drought, resulted in sharply reduced populations (Goodwin 1982, 1983). Releases were terminated when only nine birds were detected in 1982 (Levy and Levy 1984, Ough and deVos 1984). Although the feasibility of reestablishing masked bobwhite had been demonstrated, and valuable insights into the bird's habitat preferences had been obtained, the most valuable lesson learned should have been a reiteration of the bird's vulnerability to grazing and drought. A refuge managed exclusively for masked bobwhite was necessary if bobwhite were to survive in both Mexico and the U. S.

Meanwhile, conditions in Sonora were deteriorating. To evaluate the suitability of pastures that had undergone brush removal, almost 3000 pen-reared adult, immature and chick masked bobwhite had been released at three locations in Sonora, mostly between 1980 and 1982 (Brown and Ellis 1984). The success of any of these releases is doubtful, however (Mills and Reichenbacher 1982). Prospects were compromised at all 3 sites because of livestock grazing and the low quality of the birds released, none of which had received any conditioning to natural conditions.

Establishment of Buenos Aires National Wildlife Refuge

In 1985, after nearly two years of controversy and lobbying by the Audubon Society, Senator DeConcini arranged for the Buenos Aires Ranch to be purchased by the FWS as a National Wildlife Refuge for the masked bobwhite. Although reports of masked bobwhite in various parts of Altar Valley persisted, the actual presence of birds could not be verified. It thus appeared that the introduced population had died out, despite moderate and above average summer precipitation between 1981 and 1984. The hope was that the elimination of grazing would now allow new birds to survive seasons of declining population levels. A reintroduction program using the Texas bobwhite adoption technique was reinitiated in 1985 in conjunction with the total exclusion of livestock grazing (Dobrott 1990). Meanwhile, the birds persisted in fluctuating numbers on several pastures south of Benjamin Hill in Sonora, Mexico

The late 1980s and early 1990s was a time of several investigations and some optimism. The birds in Sonora had survived 7 years of drought in the 1970s and again in the 1991-93 period, were persisting with brush control, and the introduction of "light grazing" to their habitat (Camou et al. 1998). In addition to a "short-term" cattle rotation plan, 25,000 seedlings of native shrubs had been planted in cleared areas subject to disking and shredding. Some pastures were planted in bufflegrass (*Pennisetum cilcare*) and an effort was made to encourage this plant over brittlebush (*Encelia farinosa*). Attempts were also made to arrest the proliferation of cat-claw mimosa (*Mimosa laxiflora*) (Martin-Rivera et al. 2001). No pastures were set aside as livestock-free control areas, however, and bobwhite populations in Sonora generally declined despite average precipitation amounts (Camou et al. 1998). Surveys during the winter of 1990-91 showed 58 birds in four different areas including a new site near Las Tricheras (Las Cruces) (Garza-Salazar 1992).

The results of the land management practices initiated on Rancho El Carrizo and adjacent ranches were mixed. More than half of the woody shrubs planted perished, and no bobwhites were detected on the study plots despite "excellent" range conditions and a two-year rest from grazing (Martin-Rivera et al. 2001). Mule deer (*Odocoileus hemionus erimicus*), antelope jackrabbits (*Lepus alleni*) and javelina (*Pecari tajacu*) were said to have increased along with bufflegrass. The disking and other land management practices were considered a success for both livestock management purposes and bobwhite habitat (Camou et al. 1998).

The 1990s also saw a new quail biologist on BANWR and a new masked bobwhite recovery plan (Kuvlesky and Dobrott 1995). Although some of the released domestics had demonstrated an ability to overwinter, the number was such that refuge personnel feared that a self-sustaining population could not be attained without continued releases. Based on 43 calling males and other survey data, Dobrott (1990) had estimated a population of 300-500 bobwhite on BANWR – a figure that would become the mantra of refuge personnel when asked how many masked bobwhite were present. Many of these birds failed to survive the 1990-91 and 1991-92 winters, however—a setback thought to be due to raptor predation, lack of winter food and hypothermia. The answer was more releases using the same two techniques of fostering masked bobwhite chicks to Texas males and teaming chicks with older captives conditioned to living on BANWR.

The total number of bobwhite released on BANWR from 1984 to 1994 totaled 17,438, with another 40 chicks inadvertently released in the Santa Cruz Valley in 1981. No food plots were provided and no predator control conducted.

A new management plan, which called for two self-sustaining populations in Arizona and two additional populations in Sonora, was ambitious, perhaps overly so. Among the several new management efforts recommended were research into genetic testing, annual monitoring of populations, and a search for new populations. Habitat improvements included prescribed burns, the installation of guzzlers and sprinklers, and light grazing in both Sonora and on BANWR. Also included was additional research into the bird's life history and behavior, better habitat management practices, the provision of sorghum as a food plot plant was reportedly highly successful in attracting bobwhite at Rancho Carrizo in 1991 (Camou et al. 1998), and a refuge in Mexico strictly for bobwhite. Most of these recommendations were never implemented to the prescribed degree, and the results of those that were implemented, were compromised by the release of captive birds prior to any evaluation. A serious fault of the 1995 plan was to continue the release of captive birds rather than allowing overwintering populations to rise and fall with natural conditions.

Evaluations and Criticisms

One of the most innovative things accomplished by Kuvlesky was to have bobwhite mentor Fred Guthery evaluate the masked bobwhite recovery program. Both Guthery and Kuvlesky were "Aggies" from Texas A&M and familiar with bobwhite situations in that state. Guthery was an expert authority and knew Texas bobwhite as well as anyone.

Guthery noted that wild bobwhite in Sonora were better adapted to arid conditions than the released birds. He determined that heat as well as precipitation and humidity were important limiting factors, and that drought increased predation rates as well as reduced nesting success. The low dispersion rates of released masked bobwhite also reduced hatching rates and limited genetic diversity. He concluded that landscape change had been detrimental to bobwhite survival by expanding the distribution of woody plants, reducing the amount of grass cover, and increasing ground level temperatures. These same changes increased the bird's exposure to aerial predators, and reduced the diversity of herbaceous quail foods. He did not consider the presence of Lehmann's lovegrass (*Eragrostis lehmanni*) and bufflegrass as serious detriments nor was he particularly concerned about interspecific competition– issues of concern among members of the Masked Bobwhite Recovery Team.

Guthery thought that the bobwhite's primary problem was a lack of herbaceous cover and that the conservation emphasis should be in the tropical environments in Sonora. Conscious of the Mexican government's change in emphasis from agricultural production to resource utilization, he encouraged landscape restoration rather than protection as the primary conservation need. Disking and soil aeration were encouraged as were other active landscape measures including an accelerated burning program, food plots, the provision of water, and light grazing. Although well intentioned, the inability of masked bobwhite to tolerate any removal of grass cover during times of drought would bode ill for the Sonoran populations.

In an invited analysis of the masked bobwhite recovery program, Wildlife Society personnel called for a more scientific approach to recovery (Hernández et al. 2006). Overly optimistic in its assumption that recovery was underway, this report claimed among other things that biologists had never proven that masked bobwhite were not negatively impacted by brush invasion, had always experienced low reproductive rates, and had not been impacted negatively by non-native grasses. Although some of this criticism may have had some merit, the recommendations presented in Hernandez et al. 2006 were either too late or not implemented, and were proven moot with the disappearance of wild birds shortly afterward.

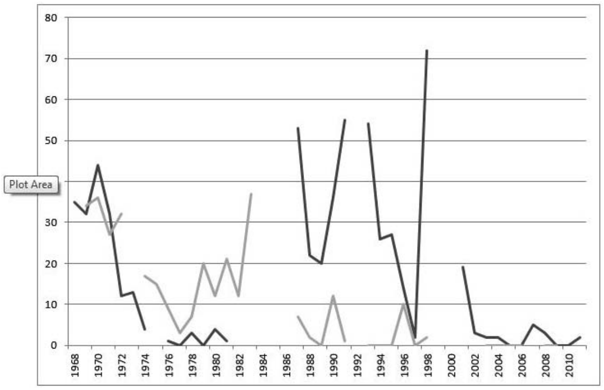

Fig. 5. Call count results from Rancho El Carrizo (dark gray) and Rancho Grande (light gray), Sonora, Mexico, 1968-2011. Data from USFWS (2014a). Gómez Limón reported the last verified masked bobwhite in Sonora as one seen and photographed in 2007. Reports since that year have not been verified.

After an uptick in the call-count surveys during the favorable year of 1999, 37 masked bobwhites were captured at Rancho El Carrizo, 25 of which were released on the central portion of BANWR (Gomez Limon 2008). Although some of these birds overwintered and reproduced based on unbanded birds being captured, captive releases were resumed the following year, both north and south of the site where the wild birds were released. This was unfortunate in that in addition to the obvious genetic problems that were becoming apparent with the captive population, these releases failed to consider the dangers posed to wild birds by the spread of such incipient diseases as respiratory cryptosporidiosis (*Cryptosporiium bailey*) found in confined gallinaceous birds (see e.g., Baines et al. 2014). Whatever the case, no masked bobwhite were documented as being heard or seen on BANWR thereafter.

Meanwhile, few land management improvements had been undertaken in Arizona and few birds, if any, detected after the year 2000. The captive population at BANWR was plagued by disease, deformities, and inbreeding. The foster parent program was abandoned due to the threats of hybridization, disease transmission, infertile birds, and the high costs involved. All releases were terminated in 2005.

Survey Efforts: 1977 - Present

The Masked Bobwhite Recovery Plan, approved in 1977, called for annual call count surveys to be conducted to monitor both the wild population in Sonora and released birds in Arizona and Sonora (Brown and Ellis 1977). Call count surveys are generally used to develop a population index to show relative size of a population, rather than actual population numbers or density. Figure 5 shows the results of call counts conducted from 1968 to 2011 on two ranches in Sonora (data from USFWS 2014a). These results show wide variability in population levels, with isolated periods of increasing populations, such as at Rancho Grande in 1977-1983 and at Rancho El Carrizo in the late 1980's to early 1990's, interspersed with longer periods of low or declining population levels. These results should be interpreted with caution however, as it is not clear if the same methods and survey effort were consistently utilized across years. The general correlation between the El Carrizo and Grande counts from 1968-1984 lends some credence to the utility of the data as a general index for the relative population levels in the region during those years. After 1984, however, results from the sites are highly discordant, and the brevity and variations in survey effort may obscure population trends during this period.

Extensive surveys in 1991 employing both winter covey surveys using dogs as well as summertime call counts found several new inhabited areas beyond the known Rancho El Carrizo population including areas to the west near Trincheras and to the south near Carbó (Garza-Salazar et al. 1992). Surveyors found bobwhite occurring on six separate ranches, plus reports of recent sightings by locals on three more ranches near Sásabe, Sonora. They concluded that populations seemed to have expanded in the Benjamín Hill area, but had disappeared in other areas, and was extremely small in the newly found site.

Surveys in the mid-2000′s focused on censusing the population at Rancho El Carrizo and surrounding areas (Gómez Limón 2008). These surveys primarily used walking routes, where an observer would look and listen for bobwhite. Some limited vehicular surveys, as well as some call playback attempts were also made. A few searches with dogs were attempted in late winter.

The results of these later surveys compared to the 1968-1982 period at both Rancho El Carrizo and Rancho Grande show that after declines in the mid-1970′s due to regional drought, population growth rises in the early 1980's, but undergoes a series of wide fluctuations in the late 1980's and 1990's before crashing in the 2000's. Camou et al. (1998) found that populations of masked bobwhite declined in 13 of 14 years when the preceding three year average of June-August rainfall was below 20 cm, and increased in 11 of 13 years when the preceding three year average was above 20 cm.

Masked bobwhite in the 21st Century

The year 1998 was characterized by record rains in the southwestern U.S. and northwestern Mexico, and masked bobwhite call counts at Rancho Carrizo reached a 30 year high (Figure 5). This boom proved to be short-lived, however, as 2002 was one of the driest years on record in the Southwest. Populations of many wildlife species crashed, including the Sonoran Pronghorn, which was reduced from 142 in 1998 to 21 individuals on the Cabeza Prieta National Wildlife Refuge in southern Arizona. Masked bobwhite fared no better, and call counts resulted in a population index near zero (Figure 5). The last confirmed sighting of a wild Masked Bobwhite anywhere was a single individual found and photographed in 2007 (Gómez Limón 2008).

Roy Tomlinson assisted in a weeklong call count survey in 2006 of the remaining habitat around Benjamin Hill. The dean of masked bobwhite field studies, Tomlinson wrote several memos comparing his observations during this survey with his experiences during his extended studies in the area in the late 1960's-early 1970's (Tomlinson 2006a, 2006b, 2006c). He criticized the lack of management for bobwhite and the overstocking of cattle "it is my impression that habitat status has declined conspicuously from the early 70's to the present. Many areas have many more trees and less grassland than before" (Tomlinson 2006b). He went on to conclude that, "I suggest that the population has been reduced to a mere fraction of that that I observed in the 1970's. It was a very discouraging result that signaled the disappearance of masked bobwhites in Sonora" (Tomlinson 2006c).

Tomlinson also lamented the lack of action on the part of U.S. conservationists to conserve any habitat for bobwhite in Mexico. He recommended completely removing cattle on select pastures that would be managed instead for mule deer hunting. He noted, "This practice would greatly benefit the quail by providing much better grass and shrub cover" (Tomlinson 2006b).

After these surveys a renewed effort by the USFWS Recovery Team led to a draft conservation plan released in 2008 (Masked Bobwhite Recovery Team 2008). This conservation plan had four goals: 1) Locate and preserve one wild, viable population of masked bobwhites in Mexico; 2) Ensure species survival through maintenance of captive programs; 3) Establish a second breeding facility in the U.S. or Mexico; and 4) prepare captive birds for release in Mexico. This document emphasized putting resources into the captive breeding program despite the first goal being the preservation of wild birds. Captive releases could not occur unless a viable population was found, and if only low numbers of wild birds were found this would necessitate releasing captive birds in areas of a remnant wild population.

Of these goals, the only one in which progress was made was in establishing an additional captive population outside of the one maintained at BANWR. By 2011, a new facility was under construction at African Safari in Puebla, Mexico (Mesta 2012). This facility is now rearing parent-reared birds for future release.

The 2008 Recovery Team Framework placed emphasis on the captive flock rather than surveys for wild birds. By 2012, USFWS refuge staff had summarized the captive breeding effort: 120 pairs bred each year with >31,000 pen-reared birds released to date of which >21,000 were released on the refuge (Cohan et al. 2012). Despite the massive time and monetary commitment to the captive flock, no wild population was ever established. Disagreement with the priorities outlined in the Recovery Team Framework led the USFWS Region 2 staff to author the *USFWS Conservation and Management of Masked Bobwhite Quail Future Direction* published in 2014. This document reinstated the expressed goal of identifying and preserving a wild population of masked bobwhite, with the captive flock reduced to serving as a safeguard against extinction (USFWS 2014b).

From 2009-2012 the authors conducted six separate survey excursions to various historical habitats in Sonora, culminating in February 2012 with a weeklong survey with dogs of the Yaqui Reservation. These lands are traditionally closed to outsiders, and we were fortunate to be given access to an area that had looked to contain high quality habitat during aerial overflight surveys (Brown et al. 2012). We did succeed in finding high quality habitat with impressive grass cover, but could locate no bobwhite. Only small portions of a vast landscape could be surveyed in our short amount of time in the field, and follow up surveys would be worthwhile.

The USFWS has dedicated funding in 2016 to conduct systematic surveys for masked bobwhite throughout the ranches of the Benjamin Hill area. Future plans include an expanded survey over much of the historical masked bobwhite range in Sonora. Parent-reared captive-bred birds from a captive breeding facility in Puebla are being readied for release in areas deemed to contain suitable habitat and found to be devoid of wild birds.

A report released by the Office of Inspector General in January 2017, documented negligence by staff of the USFWS in caring for captive masked bobwhite and not providing suitable facilities (OIG 2017). A presentation to the Masked Bobwhite Recovery Team in October 2015 showed photographs of the poor condition of the captive birds, with injuries to beaks and feet, and missing feathers due to aggressive interactions among birds in very crowded conditions. Upon learning of the presentation, USFWS staff from the Regional Office seemed as concerned with the public relations fallout as with the condition of the birds (OIG 2017). The report emphasized the lack of communication between various offices of the USFWS, and the seeming lack of direction in the Masked Bobwhite Quail Program.

Thus, nearly 10 years after the species was last seen in the wild, the USFWS and the Masked Bobwhite Recovery Team have finally agreed to systematic surveys throughout the Benjamin Hill area, and on historically suitable habitat. The results of this effort will guide if, when, and where future releases of captive bred birds may be released.

SUMMARY OF PAST RESTORATION FAILURES

The following shortcomings have been identified in past restoration attempts keeping in mind that the restoration of any race of bobwhite may be extremely difficult.

1. There has been a general emphasis and reliance on unsuitable captive-reared birds including poorly documented releases in Mexico, the interactions of which may have threatened the survival of wild birds in addition to released wild-caught birds.
2. Diversion of funding away from studies and surveys of wild birds in Mexico in favor of a captive breeding program and the release of propagated stock.
3. Failure to follow the 1984 Recovery Plan that emphasized the release of wild-caught birds and recommended the provision of food plots to increase over winter survival rates
4. The organizational structure of the U. S. Fish and Wildlife that lead to no clear command of the masked

bobwhite recovery program, the hiring of personnel, and the selection of recovery team members who were chosen not for their experience and knowledge, but to represent participating agencies.

5. Poor public relations due to poor administrative actions as not paying the travel of some but not all experts, and a lack of volunteer effort by BANWR personnel.
6. A general lack of research and natural history studies, especially of birds in Mexico
7. A haphazard monitoring of birds in both Arizona and Sonora
8. A lack of coordination and participation by Sonoran biologists, officials in CEDES, and Mexican universities.
9. Reluctance to engage volunteer bobwhite experts to find additional populations in Sonora and comment on recovery operations.

RECOMMENDATIONS

Some hope remains. A renewed emphasis on surveying wild populations of bobwhite in Mexico is under discussion, and should be implemented. Western Mexico encompasses a large area and much of it has never been surveyed for masked bobwhite. In addition, should a wild population be found, a significant area of suitable habitat should be purchased and managed for bobwhite free of livestock grazing. Excess numbers of wild-trapped birds in good years could then be used to restock historic habitats in Altar Valley and along the Santa Cruz River, which after > 30 years of rest have now had sufficient time to recover from the rigors of grazing during drought. That the characteristics of masked bobwhite habitats have been identified and are available for analysis should aid in this effort (Brown et al. 2012).

Given that bobwhite are extremely difficult birds to restore and suitable stock may no longer be available, the use of surrogate taxa should be considered. As early as 1887 Brewster recognized that *C. v. coyolcos* closely resembles *C. v. ridgwayi* and that the two spp. are nearly identical. If genetic analysis shows this subspecies or another subtropical race of bobwhite is closely related to the masked bobwhite, wild trapped birds of this taxon could provide suitable surrogates for restoration in historical habitats in Arizona. Efforts to determine these relationships are currently underway.

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BREEDING SEASON SPACE USE AND HABITAT SELECTION OF ADULT FEMALE SCALED AND GAMBEL'S QUAIL IN WEST TEXAS

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ABSTRACT

We used radiotelemetry to investigate breeding-season (1 Apr–1 Sep, 2012 and 2013) home ranges and habitat selection of adult female scaled (*Callipepla squamata*) and Gambel's quail (*C. gambelii*) in the eastern Chihuahuan Desert, Texas. Mean breeding-season home range (95% fixed kernel) for scaled quail was 145.02 ± 23.56 ha (range = 22.03–538.24 ha) and 156.32 ± 13.04 ha (range = 66.15–270.74 ha) for Gambel's quail. Mean core-use area (50% fixed kernel) for scaled quail was 31.38 ± 4.80 ha (range = 4.03–111.36 ha) and 32.87 ± 2.61 ha (range = 12.19–52.36) ha for Gambel's quail. We found evidence of home-range overlap in neighboring females in both species. Excessive drought can suppress nesting activity. However, encourage reproductive activity in both species may be encouraged by managing riparian areas to provide adequate forage and microclimatic conditions.

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Key words: breeding season, *Callipepla gambelii, Callipepla squamata,* Gambel's quail, habitat use, scaled quail

Central to the study of animal ecology is the understanding of how organisms occupy space in time. In theory, an animal should evaluate and select particular cover types that best provide the resources necessary for survival and reproduction, including access to food, suitable breeding areas, and protection from predators (Liao et al. 2007). Thus, based on the quality of resources provided, one would expect certain cover types to be used disproportionately relative to their availability (Johnson 1980, Thomas and Taylor 1990).

Home range has been defined as the space in which an individual conducts its normal daily activities (Burt 1943). Further, Samuel et al. (1985) defined the core area as the area within the home range that is used more frequently and receives the most concentrated use. Space use and habitat selection may not be constant throughout the life of an animal and may vary in response to season, age, population density, and overall habitat quality (Orians and Wittenberger 1991, Pulliam and Danielson 1991, Mysterud and Ims 1998). Hence, habitat selection can be defined as a hierarchical process involving a series of behavioral responses that may result in this disproportionate use of one cover type over others (Hutto 1985, Block and Brennan 1993, Jones 2001). Understanding patterns of habitat selection and space utilization is a critical step in understanding the ecology of a species within a given environment.

Habitat selection and use of space by northern bobwhites (*Colinus virginianus*) has been extensively studied in a variety of landscapes (Wilkins and Swank 1992, Tonkovich and Stauffer 1993, Dixon et al. 1996, Williams et al. 2000, Parnell III et al. 2002, Singh et al. 2011) but similar published information regarding scaled (*Callipepla squamata*) and Gambel's quail (*C. gambelii*) is sparse (Goodwin and Hungerford 1977, Bristow and Ockenfels 2006), particularly for the eastern Chihuahuan Desert. Although ecological processes are known to operate at varying spatial scale, previous studies have focused on habitat selection at one spatial scale, potentially creating misleading inferences about overall habitat selection (Johnson 1980, Orians and Wittenberger

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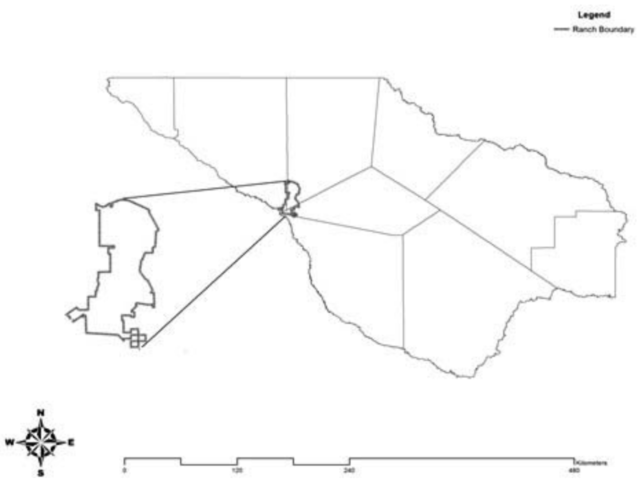

Fig. 1. Regional map of the Trans-Pecos, Texas, USA, including the Lado Ranch study site, Culberson County, where we investigated breeding-season (1 Apr–1 Sep, 2012 and 2013) home ranges and habitat selection of adult female scaled and Gambel's quail.

1991). Landscape characteristics and resource availability are important factors that influence bird communities.

As such, our objective was to estimate space use and multiscale habitat selection during the breeding season for adult female scaled and Gambel's quail in a desert scrubland in the eastern Chihuahuan Desert. The behavior of these species in a mixed desert shrubland system with wetter areas may differ from their upland and riparian counterparts. Consequently, information gathered from upland and riparian systems may not apply to a mixed desert shrubland with riparian areas. We hypothesized that, in sympatry, scaled and Gambel's quail will show different habitat selection patterns. Establishing this information in this region is necessary for managers to determine whether management considerations for one species will also be effective for the other species.

STUDY AREA

We conducted research on a 37,636-ha private ranch (hereafter, Lado Ranch; Fig. 1) in Hudspeth, Culberson, Presidio, and Jeff Davis counties, Texas. The northern portion of Lado consists of desert flats transitioning to rolling hills with numerous draws. Southern portions include the Van Horn Mountains. Mean precipitation for the area was <30.5 cm/year with peak rainfall coming in August (NOAA 2012–2013). The annual mean temperature was 16.2° C. Elevation in the study area ranged from 1,220 to 1,296 m.

Vegetation within the Lado Ranch was diverse. Individual shrub species most commonly found on Lado included creosote (*Larrea tridentata*), tarbush (*Flourensia cernua*), mariola (*Parthenium incanum*), acacia (*Acacia* spp.), lechuguilla (*Agave lecheguilla*), prickly pear (*Opuntia* spp.), and mesquite (*Prosopis* spp.). Understory was composed primarily of blue grama (*Bouteloua gracilis*), black grama (*B. eriopoda*), tobosa (*Pleuraphis mutica*), threeawns (*Aristida* spp.), tridens (*Tridens* spp.), and sacaton (*Sporobolus* spp.). Soils primarily consisted of Chispa–Chilicotal complex, Culberspeth–Chilicotal complex, and Beach very gravelly, coarse sandy loam.

METHODS

We captured scaled and Gambel's quail using standard funnel traps as described by Stoddard (1931). We placed traps in areas frequented by quail. We placed 2–4 traps located in shade at each site ($n = 7$). We covered traps with additional vegetation clippings for thermal and predatory protection. We opened traps at sunrise, closed them during the heat of the day, and opened them again 4 hours prior to sunset. We baited traps with commercial grains including millet and cracked corn. We checked traps in midmorning and late afternoon to reduce stress, exposure to predation, and injury to captured birds. All quail were trapped in accordance with state laws under scientific permit SPR-0592-525 (Texas Parks and Wildlife Department) and Sul Ross State University Animal Care and Use Committee directives.

We leg-banded captured birds with serially numbered aluminum #6 leg bands (National Band and Tag, Newport, KY, USA). After capture, we recorded the species, gender, weight, and age of each bird and took measurements of the wing, tail, head and culmen, and tarsus. Each female scaled quail weighing >180 g and each female Gambel's quail weighing >160 g was selected for radiomarking with mortality-sensitive, neck-loop transmitters (Advanced Telemetry Systems, Isanti, MN, USA; and American Wildlife Enterprises, Monticello, FL, USA). We released all birds at the capture site immediately following processing.

Following release, we allowed quail 1 day to acclimate to the transmitter and thereafter we located them once every 1–3 days from 1 March to 1 April and at least once daily for the remainder of the breeding season. We used a hand-held 3-element Yagi antenna and an ATS R4000 receiver (Advanced Telemetry Systems). We immediately located mortality signals and identified causes of death by sign left on and around the transmitter. We staggered location times throughout the day and used results to determine individual home range, habitat selection, and survival.

We excluded from analysis individuals that died within 1 week of capture to remove any bias that may have been associated with capture mortality. We censored individuals who experienced radio failure or whose signal was lost over time. All females were captured during the spring and summer (15 Mar–15 May), so we did not segregate age classes because all individuals were either adults ≥1 year old or subadults ≤1 year old being recruited into the adult population.

We imported all locations into ARCGIS 10.1 mapping software (Environmental Systems Research Institute, Inc., Redlands, CA, USA) and converted them to point themes. We calculated kernel-density home ranges (95%) and core-use areas (50%) seasonally for each individual using GEOSPATIAL MODELING EN-

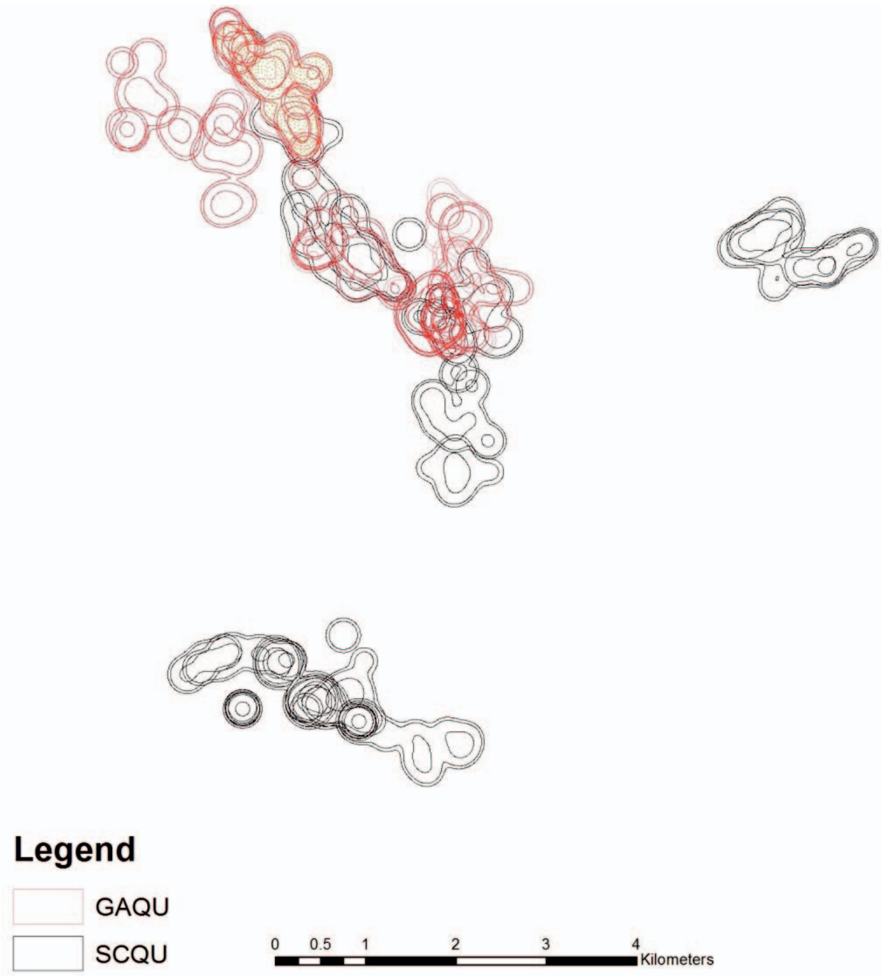

Fig. 2. Home range areas (95% and 50% Adaptive Kernel Density) of scaled and Gambel's quail at the Lado Ranch, Texas, USA, between April and September 2012.

VIRONMENT (Beyer 2012; Figs. 2 and 3). We used fixed-kernel densities as opposed to adaptive kernel to minimize overestimation of space use (Seaman and Powell 1996). We performed area-observation curves on 5 representative quail from each species with >30 locations and determined that home range sizes generally stabilized at ≥22 locations; as such, we used only individuals with ≥22 locations for analysis. We used one-way analysis of variance to test whether home range and core area sizes (ha) were different between species and years.

We created a digital land-cover map of the Lado Ranch in ARCGIS 10.1 using 2010 National Agriculture Imagery Program (NAIPs, 1-m^2 resolution) and digital elevation models (5-m^2 resolution) derived from 2010 LIDAR data (available at http://tnris.org). We delineated habitats into 3 broad categories using visual characteristics of the landscape visible on NAIPs, elevation data, and ground-truthing. Habitat types included desert grassland (lower elevation flats consisting of various gramas, tobosa grass, bluestems [*Bothriochloa* spp.; *Schizachyrium* spp.] and burrograss [*Scleropogon brevifolius*]), desert shrub (shrub-lands commonly found on hillsides and mountains adjacent to arroyos that consist of creosote bush, honey mesquite [*Prosopis glandulosa*], and tarbush), and riparian (lower elevation arroyos that consist primarily of Gregg's catclaw [*Acacia greggii*], littleleaf sumac [*Rhus microphylla*], and desert willow [*Chilopsis linearis*]). Using ARCGIS 10.1 mapping software (Environmental Systems Research Institute, Inc.), riparian habitats were defined by a 50-m buffer around all flow-line shapefiles and all other habitat not contained within the riparian habitat buffer was defined as desert grassland or desert shrub. We evaluated each scaled and Gambel's quail radio location for each habitat variable.

We intersected home ranges, core areas, and point themes with the land cover in ARCGIS to quantify habitat selection across seasons assuming that all habitats, in their respective proportions, were equally available to scaled and Gambel's quail. We calculated selection ratios (S) as $S' = ([U + 0.001]/[A + 0.001])$ where U was the observed use based on radiolocations and A was availability of the habitat variable class (Lopez et al. 2004). Aebischer et al. (1993) suggested adding 0.001 to use and availability to avoid 0 in the numerator or denominator. We described quail habitat use as preferred when selection ratios were ≥1 and avoided when selection ratios were <1 (Lopez et al. 2004). We evaluated habitat selection ratios at 3 spatial

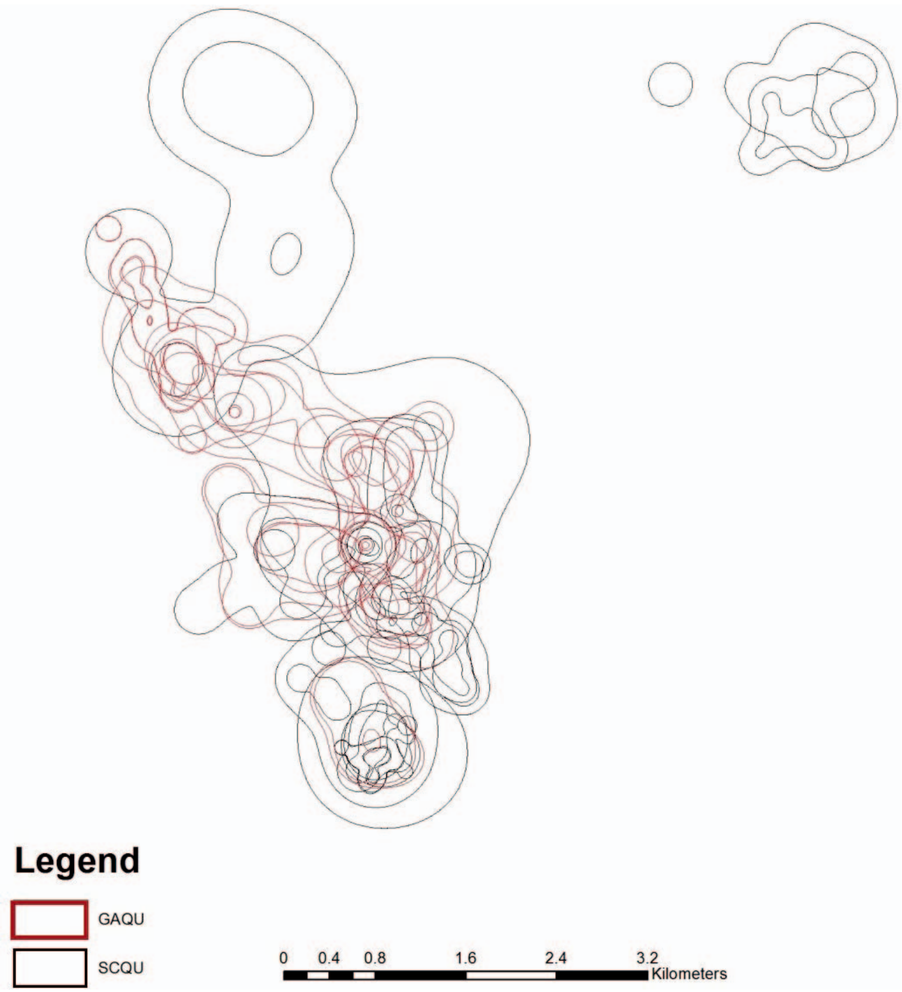

Fig. 3. Home range areas (95% and 50% Adaptive Kernel Density) of scaled and Gambel's quail at the Lado Ranch, Texas, USA, between April and September 2013.

scales based loosely on the recommendations of Johnson (1980): home ranges vs. habitats available on the study area (first order); core use areas vs. habitats available in home ranges (second order); and individual locations vs. habitat available in home ranges (third order).

RESULTS

Home range size for scaled and Gambel's quail did not differ across seasons (scaled: $F_{1,18} = 0.98$, $P = 0.33$; and Gambel's: $F_{1,18} = 0.22$, $P = 0.65$) or between species ($F_{1,24} = 0.17$, $P = 0.68$). Similarly, core area size did not differ across seasons ($F_{1,18} = 1.28$, $P = 0.27$; and $F_{1,18} = 0.98$, $P = 0.33$) or between species ($F_{1,24} = 0.55$, $P = 0.47$). During both years, the home range of every study animal was overlapped by the home range of >1 other study animal. Each study animal's home range also overlapped the home range of ≥ 1 collared individual of the other species.

For the 2012 breeding season, the average home range was 151.27 ± 66.66 ha and 129.15 ± 25.08 ha for scaled and Gambel's quail, respectively. During the 2013 breeding season, the average home range was 95.84 ± 8.27 ha and 105.04 ± 9.38 ha for scaled and Gambel's quail, respectively (Table 1; Fig. 4). The largest home range estimated for scaled quail was 538.24 ha for 2012 and 166.97 ha for 2013; for Gambel's quail, it was 235.44 ha for 2012 and 179.59 ha for 2013.

Table 1. Breeding season characteristics ($\bar{x}$ ± SE) of radiomarked scaled and Gambel's quail including adaptive kernel and 95% home ranges (HR) and 50% core area (CA) at Lado Ranch, Texas, USA, 2012 and 2013.

	Scaled quail		Gambel's quail	
Variable	2012 ($n = 7$)	2013 ($n = 13$)	2012 ($n = 7$)	2013 ($n = 12$)
CA (ha)	33.51 ± 13.52	23.32 ± 2.47	27.23 ± 4.64	24.65 ± 2.02
HR (ha)	151.27 ± 66.66	95.84 ± 8.27	129.15 ± 25.08	105.04 ± 9.38

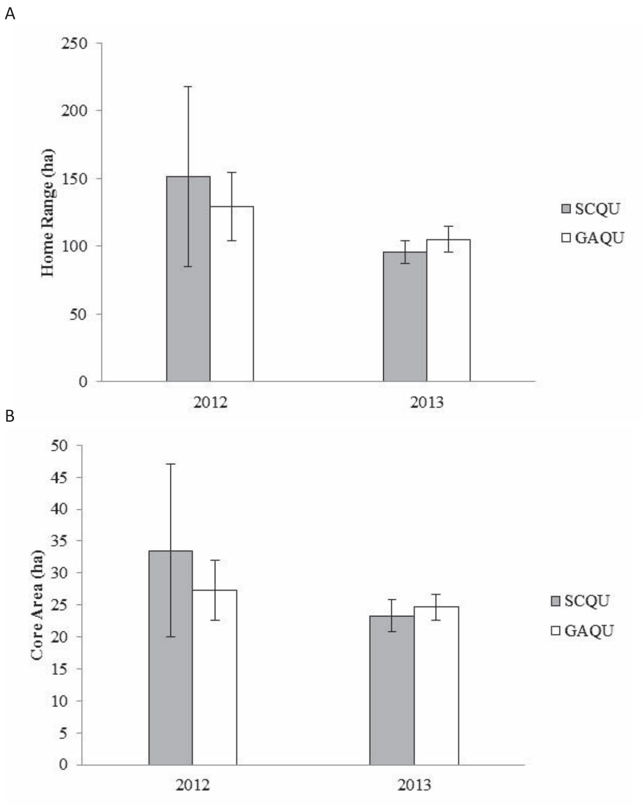

Fig. 4. Means and 95% confidence intervals of (A) 95% and (B) 50% home-range sizes of adult female scaled and Gambel's quail during the 2012 and 2013 breeding seasons Culberson County, Texas, USA.

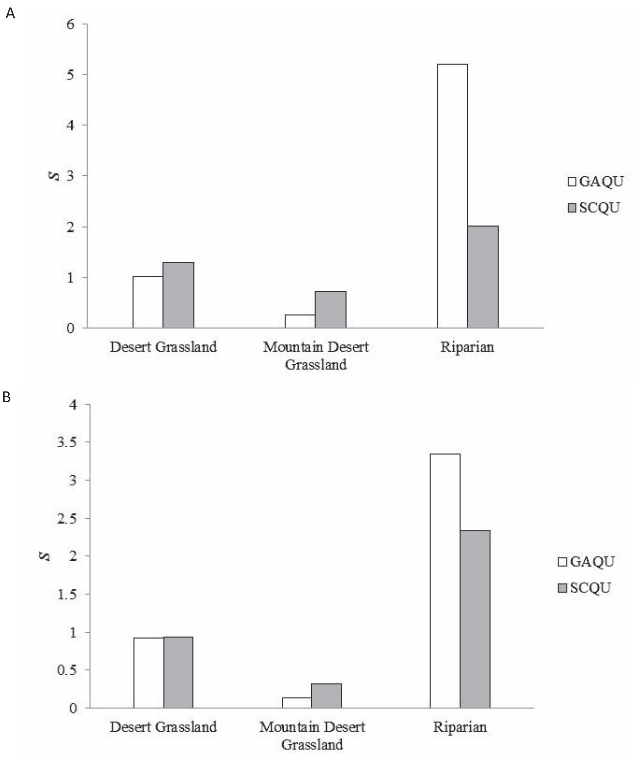

Fig. 5. Third-order habitat selection by scaled and Gambel's quail during the 2012 (A) and 2013 (B) breeding season in Culberson County, Texas, USA.

For the 2012 breeding season, the average core area was 33.51 ± 13.52 ha and 27.32 ± 4.64 ha for scaled and Gambel's quail, respectively. During the 2013 breeding season, the average core area was 23.32 ± 2.47 ha and 24.65 ± 2.02 ha for scaled and Gambel's quail, respectively (Table 1; Fig. 4). The largest core area for scaled quail was 111.36 ha for 2012 and 40.70 ha for 2013; for Gambel's quail, it was 43.02 ha and 37.54 ha.

Riparian habitat on the study area was 11.5% of 4,046 total ha. From 282 locations in 2012, scaled and Gambel's quail selected for native riparian vegetation at second-order level 23.4% and 60.6% of the time, respectively. From 229 locations in 2013, scaled and Gambel's quail selected for native riparian vegetation at the second-order level 35.3% and 56.6% of the time, respectively.

For third-order habitat selection (Fig. 5), scaled and Gambel's quail individuals used riparian habitat in greater proportion to its availability ($S > 1.1$) and desert grassland in equal proportion to its availability ($S = 1.0–1.2$). Mountain desert grassland was selected the least ($S < 1.0$) by both species.

DISCUSSION

Average home ranges (95% Adaptive Kernel Density) did not differ between years or species. Core use areas (50% Adaptive Kernel Density) also did not differ between years or species. Vegetation diversity and landscape homogeneity could be partly responsible for similar home ranges. However, home range size is often interpreted as a surrogate for habitat quality (Burt 1943, Kurzejeski and Lewis 1990). As such, the increase in home range size observed during the breeding seasons may be indicative of poor nesting habitat, requiring females to sample large areas to find suitable nesting locations. However, Gray (2005) found that range sizes of Gambel's quail exceeded previous range estimates from the Mojave Desert.

Large home range sizes may also be a function of habitat structure and limited food availability during the summer months. Annual precipitation measured in Van Horn, Texas, was below average in 2012 (15.85 cm, 52% of annual average) and above average in 2013 (34.24 cm, 112% of annual average; NOAA 2012–2013). Arid landscapes can be productive ecosystems during times of adequate rainfall when succulent vegetation is widely available and adequate brooding habitat is likely abundant enough to restrict female movements when foraging and protecting broods. As such, the slight decreases in home-range size observed in this study from 2012 to 2013 may be a direct result of increased precipitation in 2013. One would expect that, at high food densities, home range sizes would decrease and be similar sized among individuals (Börger et al. 2008).

Riparian areas were selected by both species relative to desert grassland and desert shrubland at all spatial scales during the 2012 and 2013 breeding seasons. Optimal brood-rearing habitat generally contains herba-

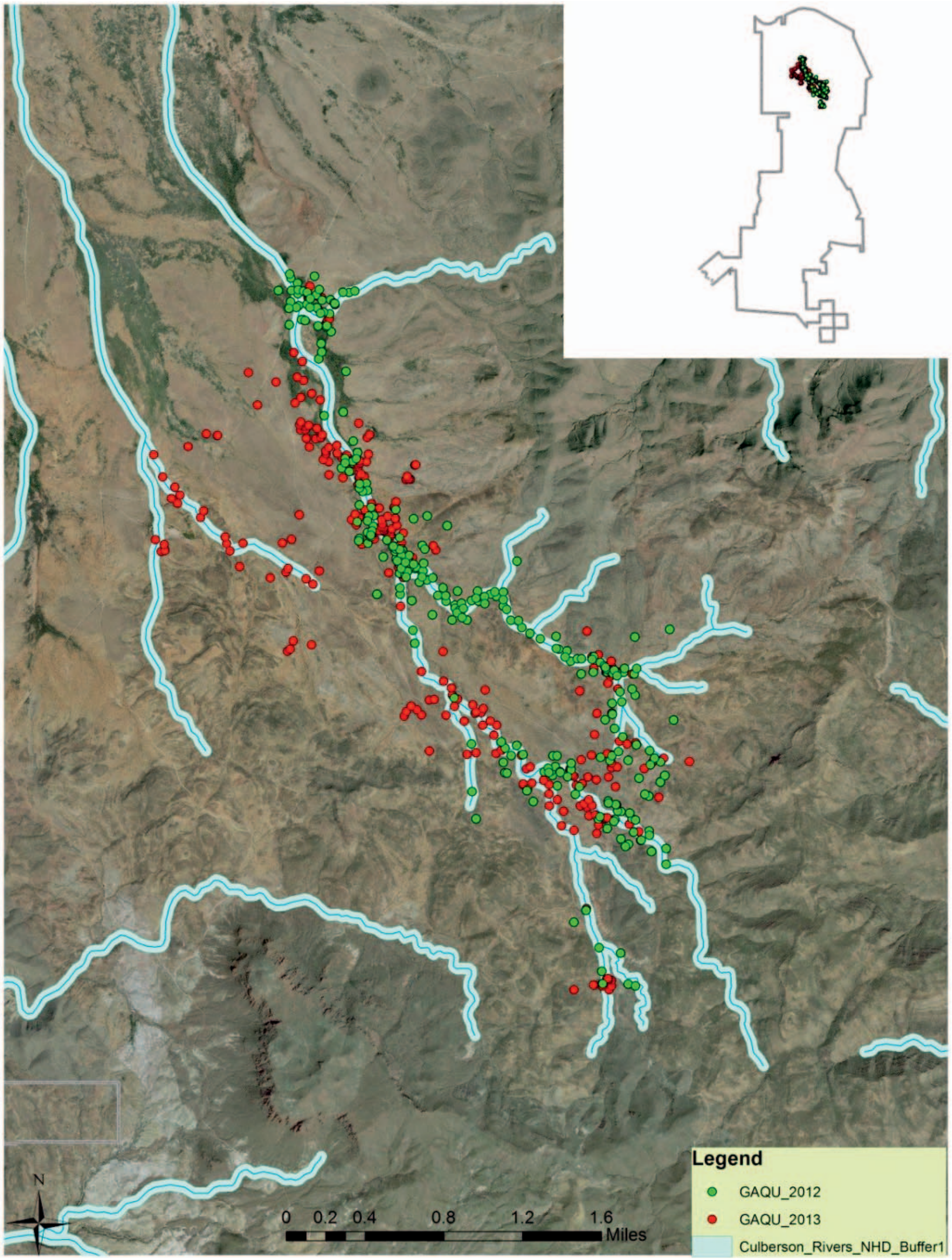

Fig. 6. Locations of radiomarked Gambel's quail and delineation of riparian habitat within the study area, Culberson County, Texas, USA, 2012–2013.

ceous ground cover that provides food resources for the nutritional needs of chicks and cover from predators. Female scaled and Gambel's quail at the Lado Ranch were likely forced to concentrate their nest site selection and movements to riparian areas because these areas provided the best brood-rearing habitat during severe drought (Figs. 6 and 7). During both years, home ranges of every radiomarked quail overlapped the home range of >1 other study animal. However, overlapping core areas between collared quail were less common than overlapping home ranges. The results did not support our initial predictions. However, because of the small sample sizes and relative difficulty of tracking quail, differences in home-range size may not have been detectable.

Home ranges link animal movements to the distribution of resources necessary for survival and reproduction (Börger et al. 2008). Competition theory states that 2 species with similar life-history traits should partition resources when sympatric (Hardin 1960, Brunjes et al. 2009). However, this does not appear to drive habitat partitioning between these 2 species. Similar home-range sizes may be a direct result of sympatry because both species co-exist on the same resources.

MANAGEMENT IMPLICATIONS

The degree of home range similarity and overlap suggests that habitat management for one species is likely

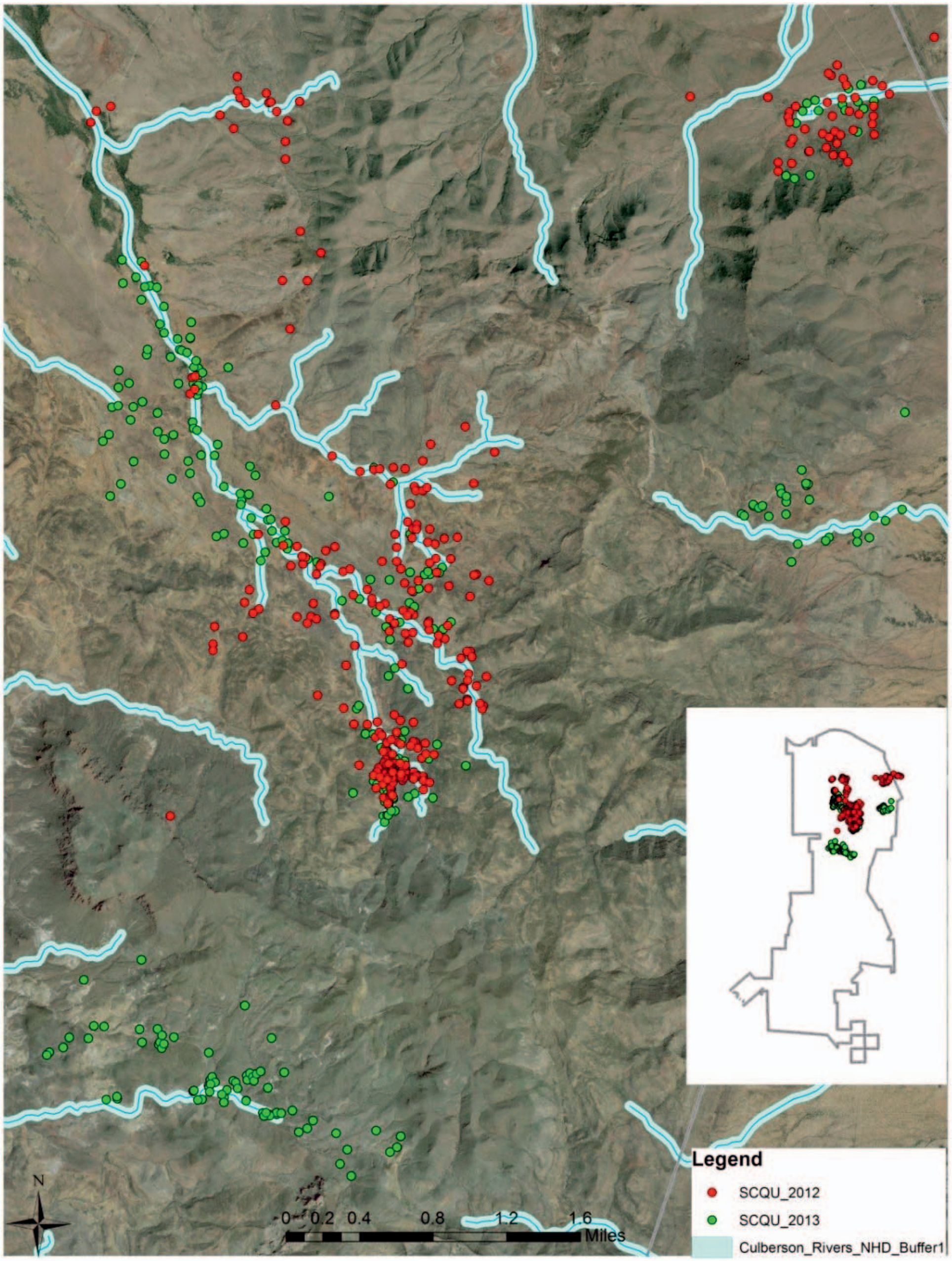

Fig. 7. Locations of radiomarked scaled quail and delineation of riparian habitat within the study area, Culberson County, Texas, USA, 2012–2013.

to benefit both species. As such, riparian habitat should be managed primarily to benefit both species through increased thermal cover and diversity. Excessive drought can suppress nesting activity of scaled and Gambel's quail; however, these riparian areas may encourage reproductive activity in both species by providing adequate forage and microclimatic conditions for broods.

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THE IMPORTANCE OF REGIONAL AND LANDSCAPE CONTEXT AND CLIMATE CHANGE TO NORTHERN BOBWHITE MANAGEMENT

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ABSTRACT

Long-term declines in northern bobwhite (*Colinus virginianus*) in the United States are presumably due to decades of habitat loss or degradation at a national scale. Food and fiber production characterized by replacement of open woodlands and savannas by dense forest, intensification of agriculture, and conversion of native grasslands to nonnative pastures have degraded habitats for most grassland and early successional birds. Declines in bobwhite and associated species occurred within this context at a scale that has overwhelmed wildlife management efforts. However, with understanding of scale and context, managers could sustain these species in some future landscapes. Increasing urbanization over the next century will result in loss of millions of acres of forests, grasslands, and agricultural lands used by bobwhite and associated species, and climate change will affect abundance and distribution of shortleaf (*Pinus echinata*), loblolly (*P. taeda*), and longleaf (*P. palustris*) pine woodlands. I highlight modeling tools and planning efforts that demonstrate how conservation planning can address these changes. I suggest that focusing management in the correct landscape contexts and accounting for land use and climate change is more likely to be successful than management that does not and conservation partnerships and management efforts across public and private lands are required to affect regional bobwhite populations.

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Key words: climate change, *Colinus virginianus,* LANDIS, landscape context, land use, northern bobwhite, prairie warbler, restoration, *Setophaga discolor*

Northern bobwhite (*Colinus virginianus;* hereafter, bobwhite) populations have declined consistently at a rate of 4%/year since 1966. Abundance measured by the North American Breeding Bird Survey (BBS) in 2013 averaged 8 birds/route, which is only 16% of the 50 birds/route in 1966 (Sauer et al. 2014). As bad as this decline is, it is not unique: 64% and 48% of grassland and early successional or scrub breeding birds, respectively, also exhibit significant declines based on the BBS (Sauer et al. 2014). It is generally accepted that long-term declines in bobwhite and many associated species are due to habitat loss, fragmentation, or degradation at a national scale (Brennan and Kuvlesky 2005, Hernández et al. 2012). The replacement of open woodlands and savannas by dense forest, the intensification of agriculture, and the conversion of native grasslands to pastures of exotic forages have degraded habitats for bobwhites and most grassland and early successional birds (Hernández et al. 2012, National Bobwhite Technical Committee 2012). These processes have taken decades and occurred throughout the United States and were driven by the economics of food and fiber production.

The ecological, landscape, and societal changes driving declines in bobwhite and associated species have often overwhelmed local and limited wildlife-management efforts. Management focused only at the local scale needs to be very intensive, sometimes including supplementation of populations and predator control, to sustain huntable populations of bobwhites. It will likely require many years of landscape-scale habitat restoration to halt the regional decline of bobwhites. It will require purposeful management and habitat restoration on public and private lands in agriculture, grassland, and forest, and include practices such as prescribed fire to return disturbance to these landscapes (Hernández et al. 2012, National Bobwhite Technical Committee 2012). The National Bobwhite Conservation Initiative 2.0 (NBCI) is a range-wide plan for recovering bobwhites (National Bobwhite Technical Committee. 2012). The NBCI is a landmark in bobwhite conservation because it provides a starting point for conservation planning. It includes a tool to aid planning and implementation of conservation at national, regional, state, and local scales. It identifies high, medium, and low-priority areas for bobwhite restoration to help agencies and organizations more effectively target management. I believe this type of multiscale, regional-to-landscape approach to prioritize areas where restoring adequate habitat is possible and landscapes are capable of sustaining bobwhite populations is critical to bird conservation in general (Probst and Gustafson 2009) and is certainly applicable to bobwhites. These ideas are not

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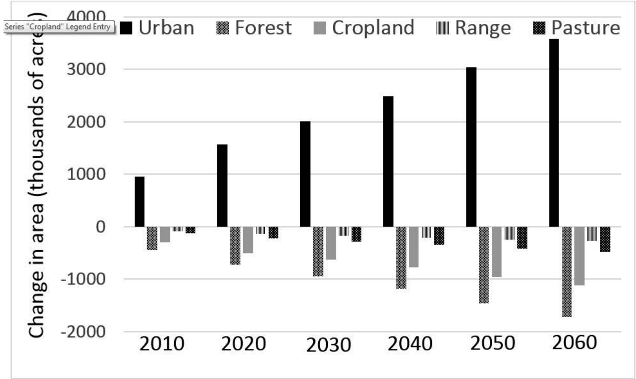

Fig. 1. Changes in urban, forest, cropland, range, and pasture land use in the southeastern United States 2010–2060. Values are averaged across predictions for the 4 Cornerstone futures developed in the Southern Forest Futures Project (Wear and Greis 2013).

necessarily new to bobwhite management; others have stated in various ways the need to have landscapes with enough habitat preserved through time to provide a critical mass of bobwhites to sustain a population (Stoddard 1931, Guthery 1997, Brennan 2011).

The NBCI provides a great foundation for bobwhite conservation because it addresses the importance of landscape context but it also provides a framework for continual improvements to its conservation planning tool. Among several of the suggested areas for improvement in NBCI are planning for climate change and urban growth and incorporating other grassland species (e.g., Butler et al. 2017, Joos et al. 2017) to optimize conservation efforts (National Bobwhite Technical Committee 2012). Future landscape- and regional-scale changes in forests, agriculture, urbanization, and climate will provide great challenges to bobwhite conservation.

Although landscape change and habitat loss are important drivers of present-day species declines and extinction (Sodhi et al. 2009), climate change is expected to become equally or more important in the coming decades as it interacts with these threats (Brook et al. 2008, Rodenhouse et al. 2008, Stralberg et al. 2009). Climate change has been called the single biggest threat to birds with more than half of bird species in North America at risk of losing more than half their current geographic range (National Audubon Society 2015). The indirect effects of climate change on forest ecosystems will result in habitat changes for birds across the eastern United States (Rodenhouse et al. 2008, Matthews et al. 2011). Furthermore, climate change will interact with important ecological process that also affect bobwhite habitat, such as fire (Guyette et al. 2014).

Here, I briefly review how 3 important aspects of regional and landscape context—climate, land use, and forests—are projected to change over the next 60–100 years within the core of the northern bobwhite range. I then demonstrate how conservation that acknowledges these aspects of context and scale can be more effective at sustaining grassland and shrub-scrub species than management that ignores these factors. I do this by reporting on some modeling tools and planning efforts that demonstrate how management that accounts for landscape context and acknowledges succession, management, urbanization, and climate change is more likely to be successful than management that ignores these factors.

CHANGES IN THE REGIONAL CONTEXT: CLIMATE AND LAND USE

The Southern Forest Futures Project forecasted changes in the South's climate, land use, and forests over the next century and provides a valuable assessment of factors that will influence conservation of northern bobwhite and associated species (Wear and Greis 2013). The project is focused on 13 southeastern states from Virginia to Texas and therefore covers much of the northern bobwhite range. The project constructed forecasts based on a set of 4–6 future scenarios that included assumptions about economic growth, population growth, climate, timber prices, and forest planting to the year 2060. Although the original results are presented by scenario, I averaged model results across scenarios to provide an overview of these forecasted regional changes in climate and land use.

The climate change summaries presented in the Southern Forest Futures Project are based on 4 different climate models (MK2, MK3.5, HadCM3, and MIROC 3.2) and 2 different emission scenarios (A1B, B2) from climate predictions by Intergovernmental Panel on Climate Change (IPCC 2007, Wear and Greis 2013). On average, the south is expected to experience warmer temperatures in the future but precipitation patterns vary with model and scenario from wet and warm to dry and hot. Recent historical climate (2001–2009) had an average annual temperature of 16.97° C and 1,136 mm of precipitation. The forecasted average annual temperature and total precipitation in 2090 range from 20° to –22° C and 860 to 1,220 mm, respectively, depending on scenario (Wear and Greis 2013). However, these averages can be misleading because climate forecasts, especially precipitation, vary spatially (e.g., under 2 of the scenarios, portions of the region experience >20% decreases in precipitation). As I discuss later, these changes have the potential to affect ecosystem productivity and affect distributions of tree species that influence wildlife habitat.

Although the impacts of regional climate change on northern bobwhite may be difficult to assess, the effects of land use change are more directly apparent. Simply put, any land use that is of any value to northern bobwhites and associated species will decline over the next century. The amount of urban land is projected to double by 2060 from a base of 30 million acres (approx. 12,000,000 ha) in 1997, expanding from approximately 7% to 13–16% of the region. Although this increase comes at the expense of forest, cropland, range, and pasture (Fig. 1), the total loss of forest area is forecasted to range from 4 to 21 million acres (approx. 1,600,000 to 8,500,000 ha; 2–10%) by 2060 (Wear and Greis 2013).

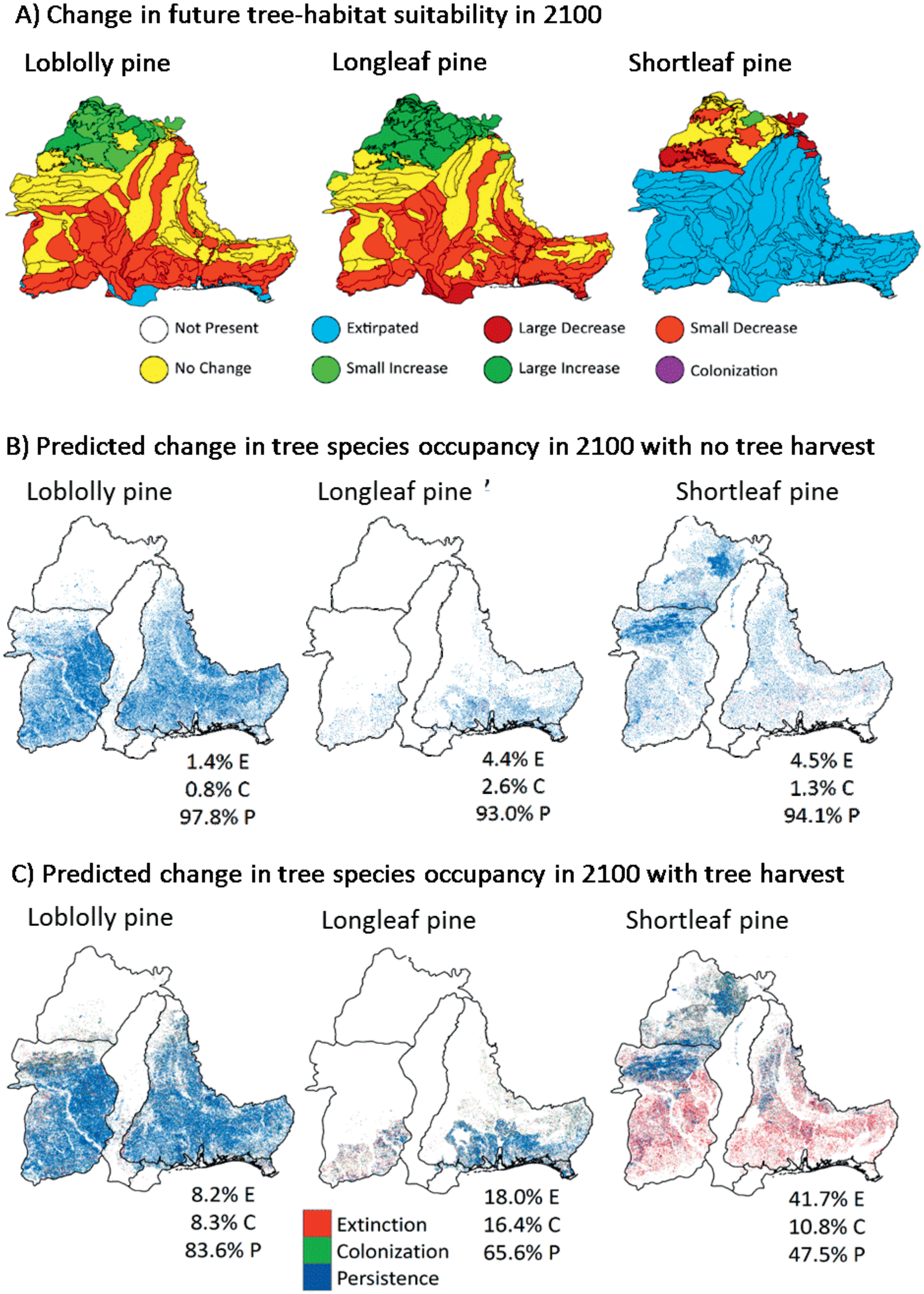

Fig. 2. Predicted changes in (A) tree habitat suitability and (B) tree species occupancy in 2100 without tree harvest, and (C) tree species occupancy in 2100 with tree harvest under climate change in the Gulf Coast Plains and Ozarks region of the southern United States. Changes in habitat suitability are based on early growth and survival of trees simulated by LINKAGES 3.0. Predicted tree species occupancy are based on forest landscape change simulations with LANDIS PRO and include current levels of fire and tree harvest or no tree harvest. Results presented are for the CanESM2 RCP 8.5 scenario, which represented an intermediate level of climate change compared with the other 2 scenarios considered (He and Thompson 2016).

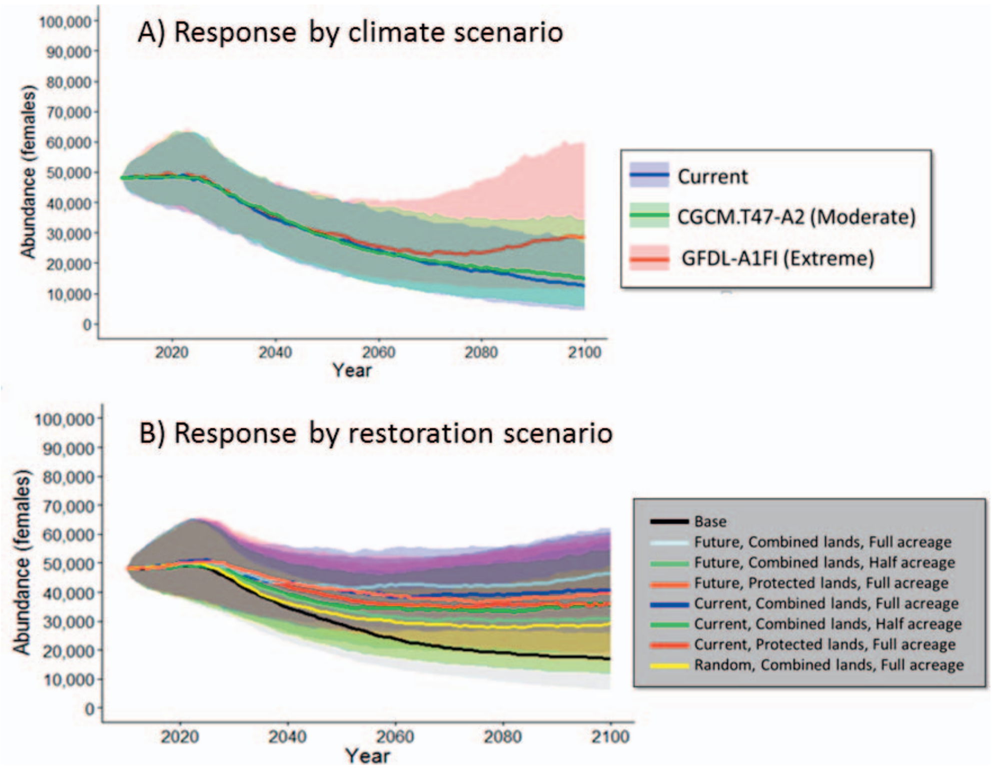

Fig. 3. Projected population growth of prairie warbler population in the Ozark Highlands (A) by climate scenario but with no habitat restoration and (B) by habitat restoration scenario averaged across climate scenarios. Shaded regions indicate 85% credible intervals. Predictions are based on dynamic-landscape metapopulation models applied to landscapes projected under urbanization and current climate, moderate (CGCM.T47-A2), and extreme (GFDL.A1Fi) climate change. Habitat restoration scenarios vary by whether restoration is located based on future or current landscapes, or random; occurs on public, private, or combined lands; and no restoration (base), half, or full acreage is implemented; see Bonnot et al. (2016) for details.

The same drivers affecting land use will also have implications for the types of forest uses. Changes in hardwood forests were most influenced by urbanization, whereas changes in softwood types were most influenced by timber markets. Land use changes and conversion to pine (*Pinus* spp.) plantations is predicted to increase the area of planted pine while decreasing the area of naturally regenerated pine. At present planted pine comprises approximately 19% of southern forests but by 2060 it could represent 24–36% of southern forests. Upland hardwood forest are forecasted to decrease 8–14% (Wear and Greis 2013).

CHANGES IN LANDSCAPE CONTEXT

I have been working with a team to investigate the effects of climate change, urbanization, and forest management on forest landscape change and selected wildlife focal species in the Gulf Coastal Plains and Ozarks (GCPO) and Central Hardwood Forest Region (Wang et al. 2015, Bonnot et al. 2016, He and Thompson 2016). The GCPO is a 180-million acre (approx. 72,800,000 ha) region that includes portions of Texas, Oklahoma, Missouri Arkansas, Louisiana, Mississippi Illinois, Kentucky, Tennessee, Alabama, Georgia, and Florida; it is in the heart of the northern bobwhite range. Here I present our approach and some findings because they provide insight into landscape changes and context that are particularly relevant to northern bobwhite and are an example of how these drivers of landscape and wildlife population change can be integrated into conservation planning at a scale that can make a difference to regional wildlife populations.

We used a modeling framework to address climate change, urbanization, and management impacts on 29 tree species over the next 100–300 years in the GCPO (He and Thompson 2016). Our modeling framework couples the forest landscape change model LANDIS PRO (Wang et al. 2014, 2015) with the forest ecosystem model LINKAGES 3.0 (Dijak et al. 2017) and downscaled climate forecasts from several scenarios and general circulation models from the fifth phase of the Coupled Model Intercomparison Project (IPCC 2014). We account for urban growth by using urban growth projections for the southeastern United States based on the SLUETH model (Belyea and Terando 2015). We determined changes in tree habitat suitability as the ratio of future to current early growth and survival of tree species (measured as biomass for years 1–30) from LINKAGES predictions (Dijak et al. 2017, Iverson et al. 2017). We used LANDIS PRO to simulate the impacts of scenarios that included different levels and combinations of climate change, forest management, and urbanization on tree species basal area, density, importance value, and occurrence in the region over the next 100–300 years. A key feature of this framework is it allows comparison of change in future habitat suitability for trees under climate change based on the LINKAGES model with the actual forecasted change in tree species abundance and occurrence as affected by succession, disturbance, management, and climate simulated by LANDIS; these often differ because trees are long-lived and have limited dispersal abilities (Wang et al. 2015, Iverson et al. 2017).

Key findings from the Linkages model were the general movement northward of potential habitat for most species. The extent of this was great enough for some species, such as sugar maple (*Acer saccharum*) and white oak (*Quercus alba*), that it implied their near potential extirpation from the region. However even common species saw decreases in habitat suitability in the southern part of the region. For example, habitat suitability for loblolly (*Pinus taeda*) and longleaf (*P. palustris*) pine decreased in the southern part of the region, no change in the Ouachita Highlands, and increased in the Ozark Highlands. Shortleaf pine (*Pinus echinata*) had zero habitat suitability in much of the southern part of the region and the Ozark Highlands was a mix of decrease, no change, and increase (Fig. 2A). Another important finding was the reduction in tree carrying capacity, expressed as the ratio of current to future maximum biomass, for varying extents of the region depending on the climate scenario. Reductions in tree carrying capacity could represent shifts in sites from forest to woodland or savanna.

The LANDIS model simulations generally confirmed that species with the greatest predicted loss in potential habitat had the greatest realized change over the next 100 years. For example, loblolly and longleaf pine persisted across most of their current range and extinction events were balanced by colonization events, with or without tree harvest (Fig. 2B, C). However with tree harvest shortleaf pine went extinct on 41.7% of pixels while it only colonized 10.8% and extinctions were concentrated across the southern part of the region (Fig. 2C). The role of harvest or management was very important because it provided the opportunity for forest turnover to more adapted species under future climates, which was particularly evident in the increase in extinction events for shortleaf pine from 4.5% to 41.7% when tree harvest was included (Fig. 2C). In other scenarios not summarized here we demonstrated how planting could greatly increase shortleaf pine woodland in the Ozark Highlands under future climates (He and Thompson 2016).

So what is the relevance of all this to northern bobwhite and other associated species? Interest in the value of pine woodlands, especially longleaf and shortleaf pine, for wildlife has risen in recent years (GCPO Open Pine Projects, http://api.ning.com/files/AgFOgF-tqnT8VX2dQgzdApbW98ZiEu*nvjJsWQ3WCOod558hPRQR1l2QoDNPmaQwkB8zJVzgoJG9jtZ-hHGdW02w*mf*utSi/InActionOpenPineFACTSHEET62915.pdf). Our models demonstrate potential shift in the amount of and location of these ecosystems. On the negative side there could be a loss of shortleaf pine throughout much of the southern part of the region. On the positive side there is the potential for a transition of some forest to woodland and an increase in loblolly and shortleaf pine woodland in the Ouachita and Ozark regions. Importantly, He and Thompson (2016) also demonstrate how management can be used to achieve objectives of forest-land management while accounting for climate change. So although papers in this symposium address how to manage longleaf pine in current landscapes for northern bobwhite and associated species (Butler et al. 2017, Rosche et al. 2017, Terhune et al. 2017), considering how to encourage its establishment in future suitable landscapes will be necessary if climate warms to the extent predicted.

In addition to its effect on vegetation, climate change can affect bobwhite survival, abundance, and distribution directly. Lebrun et al. (2016) related bobwhite abundance on North American Breeding Bird Survey routes to weather and land cover variables; abundance was positively related to average winter temperature and negatively related to average winter precipitation. Lebrun et al. (2017) used these relationships to predict changes in bird abundances, including bobwhites, for southern Missouri over the next 100 years in response to management and climate change. Bobwhite abundance increased 33% under the scenario that assumed management as usual and climate based on the Hadley Centre Coupled Model version 3 with A1fi emission scenario, which projected a 3.13° C increase in mean winter temperature. Although LeBrun found relationships with seasonal mean temperatures, the mechanisms behind these relationships are likely at least partly due to finer scale temporal and spatial relationships with climatic extremes. For example bobwhite space use is constrained by extreme heat (>35° C) and cold (<15° C) and survival reduced by weekly periods of extreme cold (Tanner et al. 2016). So direct effects of climate warming could increase winter survival of birds in northern parts of their range but have negative consequences for birds in the southern parts of their range.

INCORPORATING LANDSCAPE AND CLIMATE CHANGE IN WILDLIFE CONSERVATION PLANNING

Bonnot (2016) integrated the climate and landscape change modeling framework described above with a wildlife meta-population model (Bonnot et al. 2011, 2013) into a dynamic landscape metapopulation model (DLMP) and demonstrated how this approach can be used to forecast effects of climate change, succession, and land management on regional wildlife populations. Bonnot et al. (2016) used the DLMP approach within a structured decision-making framework to demonstrate its usefulness in overcoming the uncertainties and complexities that are inherent in the process of long-term, large-scale conservation planning, especially when it involves climate change. I review some of their results here because they examined several species associated with northern bobwhites, and there are ongoing efforts to apply this approach to northern bobwhites. Furthermore, it illustrates that large-scale conservation planning, when it addresses landscape context, can reverse population declines.

The DLMP approach is based on matrix-based population models in which demographic parameters such as carrying capacity, productivity, and survival are linked to attributes of the habitat patch in which a subpopulation resides. Patches change over time, as simulated by the forest landscape change model LANDIS, and forest landscape change can be affected by climate effects on the establishment and early growth of trees as predicted by the LINKAGES model. Bonnot et al. (2016) applied this approach to the Ozark Highlands, a subregion within the GCPO, to evaluate 8 habitat restoration scenarios under 3 climate scenarios. The scenarios were spatially explicit plans for restoration of 1.5 or 3 million acres (approx. 607,000 or 1,210,000 ha) of glades, woodlands, and forest. These activities were targeted on either private, public, or private and public lands, and areas were prioritized based on current landscapes or future landscapes accounting for urbanization and climate change. All scenarios also included current levels of forest management and fire and wind disturbance.

Bonnot et al. (2016) predicted impacts on 6 focal species but here I focus on results for the prairie warbler (*Setophaga discolor*) because it breeds in many of the same vegetation communities that provide high-quality habitat for northern bobwhites (e.g., shrub-scrub, glades, woodlands) and both species respond positively to fire. In the absence of habitat restoration (but with current the level of forest management and fire) and under current climate, prairie warbler populations continued to decline at a rate consistent with recent historical declines (Fig. 3A). This decline was largely the result of forest succession resulting in more mature forests with more closed canopies, which reduced carrying capacity. However, under 2 climate change scenarios, reduced precipitation and warmer temperatures began to affect forest structure and resulted in more open canopies by the end of the century and, after an initial period of decline, the prairie warbler population began to increase near the end of the century (Fig. 3A). Habitat restoration interacted with climate change to produce interesting effects as well; prairie warbler abundances were twice as great under some restoration scenarios compared with the base scenario with no habitat restoration (Fig. 3B). Prairie warbler populations rebounded better when areas for restoration accounted for climate change and urbanization. Interestingly increases were only in part due to an increase in carrying capacity but also substantially due to more of the population residing in more favorable landscapes with less fragmentation and greater productivity—in other words, better landscape context. Reversing population declines also required restoration on both public and private lands because acreage targets could not be met on public lands alone. The Greater Red Hills region of northern Florida and southern Georgia is a real world example of how intentional management for northern bobwhite on private lands involving fire and sound forest management can result in sustained abundance at a regional level (Terhune et al. 2017).

MANAGEMENT IMPLICATIONS

My premise for these management implications and conclusions has been to highlight some recent developments in wildlife and landscape ecology that will let us take conservation for northern bobwhite and associated species to the next level. Climate change and the ensuing landscape change that will result from climate, along with other important drivers such as urbanization and land management, present substantial challenges for conservation planning. The NBCI provides a sound foundation for addressing the importance of landscape context to management. Conservation planning approaches, such as those we have worked on with the GCPO Landscape Conservation Cooperative, can provide the next steps in addressing conservation of northern bobwhite and associated species. The examples I have highlighted rely heavily on models and model forecasts, which to some extent are inaccurate, but nevertheless still useful for planning and assessment (Millspaugh et al. 2009).

These examples demonstrate several important points for conservation of bobwhite and associated species. As we lose forest, grassland, and agricultural land to urbanization, how and where we manage lands will be increasingly important (Bonnot et al. 2013). Climate will likely have important effects on the structure and composition of forests in the long term (e.g., 100–300 yr). However, management will have a much greater effect in the short term and can help either promote resilience and mitigate forest changes, facilitate change in desired directions, and determine how quickly climate-driven changes are realized. Management and restoration will likely need to occur across public and private lands to affect regional populations. However, when conservation is planned at regional scales and implemented on a large scale it can have population consequences, including reversing population declines.

Given the importance of management, one of the important factors limiting the success of bobwhite conservation is how much management and restoration we can accomplish on the ground. We are becoming more effective at landscape to regional to national planning through partnerships such as Landscape Conservation Cooperatives, the National Bobwhite Conservation Initiative, and Partners in Flight. Now, we need to establish the proposed management on the ground across multiple partners and ownerships. Efforts are underway to do this through NBCI on public and private forests and grasslands under the umbrella of management, monitoring, policy, partnerships and outreach (National Bobwhite Technical Committee 2012, NBCI 2016 SOTB, http://bringbackbobwhites.org/). Specific examples include efforts of the Wildlife Habitat Federation (http://www.whf-texas.org/) to help landowners establish native habitats for bobwhite in Texas and restoration of thousands of hectares of pine woodlands in multiple states by the U.S. Forest Service Cooperative Forest Landscape Restoration Program (https://www.fs.fed.us/restoration/CFLRP/). So to summarize in a single statement, bobwhite conservation will be more successful if we consider what the future is likely to bring and establish more management on the ground and in the correct places and NBCI is a valuable framework to guide us.

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