BREEDING BEHAVIOR, BROOD HABITAT USE,

AND CHICK SURVIVAL OF TWO QUAIL SPECIES AT

THE PERIPHERY OF THEIR DISTRIBUTIONS

By

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Abstract: One of the keys to understanding any species is acquiring a thorough knowledge of its breeding behavior and brood ecology. Until recently, little research has been conducted to understand the breeding behavior and brooding success of many quail species. As part of a larger study, I conducted research of sympatric northern bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) at Beaver River and Packsaddle wildlife management areas in western Oklahoma. Primary research objectives included: 1) investigate the survival, habitat use, and movement of northern bobwhite and scaled quail during the initial stages of their life and 2) to estimate rates of occurrence of alternative reproductive and brood-rearing strategies along with the mechanisms that may be influencing observed rates. As part of a larger project, adults were monitored daily during nesting and brood-rearing periods at two field sites in western Oklahoma to collect egg shells and feathers. Following hatching, I collected all hatched and unhatched eggshells. During capture of young chicks at 8–12 days old (chicks) and 4–6 weeks old (youths) for a survival study, I collected contour and down feathers. All samples were genotyped at a minimum of 10 species-specific microsatellite loci. Programs Colony and Genalex were used to investigate parentage and brood relatedness. During the 2013 and 2014 breeding seasons I genotyped samples from 56 nests (34 northern bobwhite and 22 scaled quail). Nest parasitism was documented in 7 (20.6%) bobwhite and 2 (9.1%) scaled quail nests. The percentage of total offspring resulting from extra-pair copulations was higher in bobwhite (29.3%) than in scaled quail (2.2%) nests. To better understand brood habitat use and chick survival, I also attached radio-transmitters to quail chicks and youths at capture. I found that the 20-day survival probability for chicks was higher in bobwhites (0.725 ± 0.068) than in scaled quail (0.488 ± 0.085), while the 35-day survival probability for youths was similar between bobwhite (0.788 ± 0.086) and scaled quail (0.795 ± 0.110). Microhabitat vegetation characteristics (angle of obstruction, shrub cover, and percent ground cover of 5 functional groups [grass, forb, legume, litter, and bare ground]) were also measured at brood locations. High levels of habitat partitioning were observed between species likely leading to observed differences in chick survival. I hope that information gained from this project will help researchers to gain an increased understanding of quail ecology.

TABLE OF CONTENTS

CHAPTER I

GENERAL INTRODUCTION

Northern bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) are economically important gamebirds throughout their distributions. Revenue from quail hunting is generated directly and indirectly from hunting leases, hunting license sales, lodging and food purchases during quail hunting, equipment related expenses, and transportation expenses associated with quail hunting (Burger et al. 1999, USFWS 2006, Hernandez and Guthery 2012). Importantly, the revenue generated from quail hunting goes to support many small rural communities and landowners. However, throughout their distributions, northern bobwhite and scaled quail are suffering from severe and long-term population declines (Brennan 1991, Sauer et al. 2014). Breeding bird survey data estimates that populations have declined at an average of 3.0% annually for scaled quail and 4.1% annually for northern bobwhite from 1966-2013 (Sauer et al. 2014). These population declines have been attributed to a wide range of factors including fire exclusion, habitat fragmentation, land use change, improper grazing, clean farming, herbicides/pesticides, urbanization, exotic species, and changes in precipitation patterns

(Brennan 1991, Schemnitz 1993, Hernandez et al. 2013). While these species are able to rebound quickly following drought years, extensive land use change and long-term droughts have led to consistent and long term population declines. It is possible that future climate change will lead to further population declines or distribution shifts for these species.

While there have been numerous studies investigating quail ecology over the last 70 - 80 years, there have been relatively few studies focused primarily on quail breeding behavior, brood habitat use, and chick survival. Moreover, the occurrence and variable rates of extra-pair paternity, nest parasitism, and brood amalgamation within northern bobwhite and scaled quail clutches have not been well studied. In order to address long-term population declines, it is important to fully understand a species breeding and brooding behavior. In order to answer numerous questions related to conservation, paternity, and brood dynamics of northern bobwhite and scaled quail I investigated the reproductive behavior and brooding success of these species at the periphery of their distributions.

Thesis Organization

This thesis is composed of three manuscripts that have been prepared for publication in scientific journals. Chapter II investigates the rates of alternative reproductive and brood rearing strategies in northern bobwhite and scaled quail. Chapter III evaluates the accuracy of brood flush counts as a method to investigate chick survival. Chapter IV investigates chick survival and brood habitat use of a sympatric population of northern bobwhite and scaled quail in western Oklahoma. In addition to the three primary chapters, a final manuscript documenting the occurrence of temporary communal brooding as a response to atypically cool temperatures has been included in the appendix.

Project Objectives

1. To determine the rates of occurrence of extra-pair paternity and nest parasitism in northern bobwhite and scaled quail broods using non-invasive genetic sampling.

2. To evaluate rates of extra-pair paternity, nest parasitism, and brood amalgamation in regard to environmental, seasonal, and population density covariates.

3. To assess the rates of occurrence of brood amalgamation in northern bobwhite and scaled quail broods.

4. To evaluate the accuracy of brood flush counts as a method to investigate chick survival.

5. To evaluate the survival and habitat use of northern bobwhite and scaled quail chicks.

6. To evaluate the influence of environmental and habitat variables on daily survival rates of northern bobwhite and scaled quail chicks.

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CHAPTER II

EXTRA-PAIR PATERNITY, NEST PARASITISM, AND BROOD

AMALGAMATION IN TWO SYMPATRIC QUAIL SPECIES: PATTERNS AND

IMPLICATIONS

Abstract

Alternative reproductive and brood rearing strategies are common across a wide

range of bird species. These strategies can take the form of extra-pair copulations, nest

parasitism, and brood amalgamations. While rates of these alternative reproductive

strategies have been well studied, the mechanisms that influence these rates across

species are not well understood. The primary hypotheses to explain variations in rates of

alternative reproductive strategies are population density, annual adult survival, and

degree of paternal care. To better understand the role these factors may play in

influencing these alternative strategies, I investigated reproductive and brood rearing

strategies in a sympatric population of northern bobwhite (*Colinus virginianus*) and

scaled quail (*Callipepla squamata*). During the 2013 and 2014 breeding seasons, I

genotyped both hatched and unhatched eggshells from 56 nests and feathers from

individuals within broods at hatch stage (0 days old), chick stage (8–12 days old), and youth stage (4–6 weeks old). Percentage of total offspring resulting from extra-pair copulations was higher in bobwhite (29.3%) than in scaled quail (2.2%) nests, with higher rates of extra-pair copulations in male incubated than female incubated bobwhite nests. Nest parasitism was documented in 7 (20.6%) bobwhite and 2 (9.1%) scaled quail nests. Differences in rates of extra-pair copulations and nest parasitism were likely a result of differences in population densities between species and years, with higher rates correlated with greater population densities. I estimated that mean intra-brood pairwise relatedness decreased significantly from the chick to youth life stages in bobwhite and scaled quail, indicating that brood amalgamations occur frequently after young become mobile and independent. Based on our results, rates of alternative reproductive and brood rearing strategies within bobwhite and scaled quail were likely influenced significantly by population density and levels of paternal care.

Introduction

Alternative reproductive and brood rearing strategies are common across avian species. These strategies can take the form of: extra-pair copulations, nest parasitism, and the brood-rearing strategy of post-hatch brood amalgamation. Extra-pair copulations resulting in extra-pair paternity within a socially monogamous species is defined as the occurrence of fertilizations by males that are not the putative father (Moller 1986, Griffith et al. 2002). This strategy has been documented in 90% of all avian species (Griffith et al. 2002). Females may engage in extra-pair copulations to (1) guard against infertility in the current social mate (Wetton and Parkin 1991), (2) maximize genetic diversity

6

(Westneat 1990), (3) locate genetically compatible mates (Kempenaers et al. 1999), (4)

obtain 'good genes' that would increase survival and fitness of offspring (Moller 1988,

Foerster et al. 2003), and (5) obtain physical resources from the territory of an individual

that is not their social mate (Wolf 1975). Although the occurrence of extra-pair

copulations have been documented for decades, the mechanisms that lead to high

interspecific variation in rates are not well understood. The three hypotheses that have

been commonly presented to explain variations in the rates of extra-pair copulations

include population density, annual adult mortality, and the degree of paternal care

(Griffith et al. 2002, Mulder et al. 1994,Wink and Dyrcz 1999, Arnold and Owens 2002).

Nest parasitism is defined as the situation in which a female lays one or more

eggs into another female's nest (Robertson et al. 1992). This can be intraspecific or

interspecific. Intraspecific nest parasitism has been reported in more than 93 altricial and

141 precocial bird species (Yom-Tov 2001). Occurrence of nest parasitism is especially

common in precocial species that have large clutch sizes, leave the nest unguarded for

extended periods of time prior to incubation, and require less care of young than many

altricial species (Sorenson 1992, Geffen and Tom-Tov 2001, Yom-Tov 2001). Nest

parasitism is a female reproductive strategy and females may engage in nest parasitism to

increase reproductive recruitment following the loss of a nest or brood (Yom-Tov 1980,

Petrie and Moller 1991). Females may also engage in a mixed reproductive strategy

whereby they parasitize nests while at the same time caring for their own young (Petrie

and Moller 1991). Additionally, during years in which females may be in poor

physiological condition or resource and nest site availability is poor, the female may

choose to lay her eggs in another female's nest and forego nesting that year (Emlen and

Wrege 1986, Lank et al. 1989). Variations observed in rates of nest parasitism across and between species are typically attributed to differences in nest density, nest-site and resource availability, and nest predation rates (Yom-Tov 1980, Eadie et al. 1988, Petrie and Moller 1991, Robertson et al. 1992, McRae 1997).

In addition to alternative reproductive strategies, alternative brood-rearing strategies are also varied and complex across bird species. Post-hatch brood amalgamation, also known as brood mixing, is a common alternative brooding strategy observed in a number of species with precocial young (Maxson et al. 1978, Strong et al. 1986, Faircloth et al. 2005, Metz et al. 2006, Wong et al. 2009). These amalgamations occur in the form of (1) adoptions in which the brooding adult passively accepts and fosters young into its brood, (2) kidnapping in which the dominant brooding adult actively kidnaps young from other broods, (3) crèching in which two or more unrelated offspring are cared for by two or more adults that they may or may not be related to, and (4) gang-brooding in which multiple broods and possibly other non-brooding adults join together into one large brood (Eadie et al. 1988, Afton and Paulus 1992, Faircloth et al. 2005, Wong et al. 2009). Occurrences of brood amalgamations have been documented in numerous avian species, but a dearth of knowledge exists regarding rates and timing of this alternative brooding strategy.

Despite the fact that these alternative reproductive and brood-rearing strategies have been well documented, much still remains unknown regarding mechanisms that contribute to the high levels of variation within reported rates of alternative strategies between and within species (Petrie and Kempenaers 1998). Efforts to predict factors that

may lead to inconsistencies in rates of extra-pair copulations and nest parasitism have been met with extreme difficulty due to inter-specific differences in reproductive behavior and confounding environmental conditions such as vegetation and population differences among sites and years. Due to the large variation in these alternative strategies, comparisons among closely related species have been recommended to explore factors that lead to variations in rates (Petrie and Kempenaers 1998).

Throughout western Oklahoma, northern bobwhite (*Colinus virginianus*, hereafter bobwhite) and scaled quail (*Callipepla squamata*) exist in sympatry in the periphery of their respective distributional ranges. These species have similar food preferences, life histories, nesting periods, and brooding behavior and exist under similar environmental and climactic conditions (Schemnitz 1964). The zone of sympatry between these two species provides a unique opportunity to examine mechanisms that may lead to high variation in rates of extra-pair copulation, nest parasitism, and brood amalgamations across and within species (Petrie and Kempenaers 1998). Objectives of this study were to (i) investigate rates of extra-pair copulations and nest parasitism in bobwhite and scaled quail clutches, (ii) investigate mechanisms that may lead to variations in rates of extra-pair copulation and nest parasitism, and (iii) investigate relatedness of individuals during three key life stages to determine importance of brood amalgamations as a brood-rearing strategy for bobwhite and scaled quail.

Materials and Methods

Ethics Statement

I obtained appropriate permissions for all research protocols. Capture and sample collection protocols were reviewed and approved by Oklahoma State University's Institutional Animal Care and Use Committee (ACUP #AG-13-2 and ACUP #AG-11-22). All efforts were made to limit handling time and minimize suffering of chicks during the capture and transmitter attachment process. The Oklahoma Department of Wildlife Conservation provided permission to conduct research at both study sites.

Study Area Description

This study was conducted at Beaver River Wildlife Management Area (WMA) and Packsaddle WMA in western Oklahoma during 2013 and 2014. Beaver River (11,315 ha) and Packsaddle (7,955 ha) WMA's are owned and managed by the Oklahoma Department of Wildlife Conservation. Management for upland game birds is a primary objective at these sites. Populations of scaled quail and bobwhite occur at Beaver River WMA, but only bobwhite occur at Packsaddle WMA.

Sample Collection

As part of a companion research project, bobwhite and scaled quail adults were captured from August – April to attach radio-transmitters. During capture, I extracted 5–10 contour feathers from the flank of all birds. Adults were tracked 5 days/week during the nesting season and nests were monitored daily following nest initiation. After eggs hatched and young abandoned the nest (about 12 hours post-hatch), I collected all

hatched eggshells to genetically assess extra-pair copulations and nest parasitism. Samples were uniquely labeled and stored in individual coin envelopes within a larger air tight Ziploc® bag along with 3–4 desiccant packets. I also collected remaining unhatched eggs, stored them in uniquely labeled sealed plastic bags, and froze them at –23° C prior to analysis.

A further objective of the companion study was to monitor survival and movements of quail broods with miniature radio-transmitters from hatch to 80 days old. This provided an opportunity to collect feathers from broods to genetically evaluate the occurrence of brood amalgamations. During capture of broods to attach radio-transmitters, I extracted 5–10 contour feathers from the flank of each bird and stored feathers in individual coin envelopes. Feathers were collected from two age groups: 8–12 day old birds (chicks) and 4–6 week old birds (youths). Additional youth samples were added to the study opportunistically. I aged youths based upon feather development and mass at capture (Smith and Cain 1984, Lusk et al. 2002). Only broods that had three or more of the youths captured were included in the study.

Laboratory Protocols

DNA was extracted using the Qiagen Dneasy Blood and Tissue Kit (Qiagen Inc., Valencia, CA) with extraction protocols for contour feathers, chick down feathers, and eggshell membranes, as described in (Bush et al. 2005). A small alteration was made to the final step for all feather samples by using 100 µl of Buffer AE instead of 200 µl. Genotyping was conducted using 11 species-specific microsatellite loci for bobwhite (Quail 3, Quail 31 Quail 44, Quail 13, Quail 30, Quail 22, Quail 23 (Schable et al. 2004)

and CV-P1F3, CV-PCF5, CV-P1A7, and CV-P1E6 [Faircloth et al. 2009]), and 12

species-specific loci for scaled quail (C023, A014, A110, C015, C009, A114, A104,

C022, A001, A022, B105, and A018 [Orange et al. 2014]). All chick, youth, and non-

nesting adult feather samples were not genotyped at Loci A018. Five percent of samples

were randomly selected and blindly re-genotyped to estimate the genotyping error rate

with the program PEDANT v 1.0 (Johnson and Haydon 2007).

One primer for each microsatellite locus was labeled with one of three fluorescent

tags (HEX, 6-FAM, and NED) and ran either individually or multiplexed in groups of

two or three. Individual Polymerase Chain Reactions were conducted in 15 µl reactions

consisting of 0.5 µl forward and reverse primers (10 µM), 9 µl True Allele® PCR Premix

(TA, Applied Biosystems, Foster City, California), 1.0 µl Bovine Serum Albumin (BSA),

1 µl dH_20, and 3.0 µl DNA (5-50 ng/µl). A 20 µl reaction was used for all multiplexes of

two. These reactions consisted of 0.5 µl of forward and reverse primer 1 (10 µM), 0.5 µl

forward and reverse primer 2 (10 µM), 14 µl TA, 1 µl BSA, and 3 µl DNA (5-50 ng/µl).

The final three primer 30 µl multiplex reaction consisted of 0.5 µl of forward and reverse

primer 1(10 µM), 0.5µl forward and reverse primer 2 (10 µM), 0.5µl forward and reverse

primer 3 (10 µM), 20 µl TA, 1 µl BSA, and 6 µl DNA (5-50 ng/µl).

The thermal profile for "Quail" primers (Quail 3, Quail 31, Quail 44, Quail 13,

Quail 30, Quail 22, and Quail 23) consisted of one cycle at 95°C for 12 min, 35 cycles at

94°C for 40 s, 57°C for 40 s, and 72°C for 30 s, followed by a final incubation at 72°C

for 4 min. The thermal profile for all "CV" primers (CV-P1F3, CV-PCF5, CV-P1A7,

and CV-P1E6) consisted of one cycle at 95°C for 5 min, 35 cycles at 95°C for 40 s, 65°C

for 30 s, and 72°C for 90 s, followed by 35 cycles of 95°C for 20 s, 60°C for 30 s, and

72°C for 90 s, followed by a final incubation at 72°C for 10 min. The thermal profile for

all scaled quail primers (C023, A014, A110, C015, C009, A114, A104, C022, A001,

A022, and B105) followed protocols described in Orange et al. (2014).

PCR products were electrophoresed using size marker Rox400HD on either an

ABI3130 or ABI 3730 Genetic Analyzer and scored using the Genemapper 4.0 software

(Applied Biosystems, Foster City, California). Number of alleles per locus, deviations

from Hardy-Weinberg equilibrium (HWE), observed/expected heterozygosity (H_o/H_e),

polymorphic information content (PIC) and frequency of null alleles were calculated

using Cervus 3.0.3 (Kalinowski et al. 2007). Allele frequencies were calculated using 130

adult samples (89 bobwhite, and 41 scaled quail samples).

Microsatellite Data Analyses

Program COLONY v2.0 (Jones and Wang 2009) was used to estimate number of

sires within each brood, and number of offspring that were produced from extra-pair

copulations and nest parasitism. The "polygamous" option was selected for both males

and females. Each clutch was entered as a distinct group along with the genotype of

available parentage data. The full likelihood option with "high" likelihood precision was

chosen along with a "long" length of run. Allelic dropout and genotyping error rate was

conservatively set at 0.03 based upon the maximum single locus genotyping error rate

estimated using PEDANT v 1.0 (Johnson and Haydon 2007). Using this program I

estimated the number of sires within each clutch along with the number of offspring that

were a direct result of extra-pair copulations. Additionally, mean pairwise relatedness

was calculated using GenALEx v. 6.5 (Peakall and Smouse 2012) and the Queller and

Goodnight (Queller and Goodnight 1989) relatedness calculation for all clutches,

including hatched and unhatched eggs within successful clutches ($\geq$ 1 hatched egg), for

comparisons between years and study site populations. That provided a value to estimate

combined levels of extra-pair copulations and nest parasitism within clutches and a

reliable method to investigate differences between years and species. All means are

presented $\pm$ SE and *t*-tests were used to test for differences between means. Young

resulting from nest parasitism were excluded when calculating the total proportion of

offspring resulting from extra-pair copulations. The proportion of offspring resulting

from nest parasitism and extra-pair copulations were compared with a *z*-test. Bobwhite

young (hatched and unhatched eggshells) that resulted from interspecific nest parasitism

by bobwhites into scaled quail nests were genotyped using bobwhite microsatellite loci

and thus, were not included in pairwise relatedness calculations.

To address amalgamation rates, mean pairwise relatedness within broods at the

hatch, chick, and youth life stages were calculated using the program GenALEx v. 6.5

(Peakall and Smouse 2012) and the Queller and Goodnight (Queller and Goodnight 1989)

relatedness calculation. These values were only calculated from samples collected at

Beaver River WMA because it contained sympatric populations of bobwhite and scaled

quail. Pairwise relatedness values were averaged for each species across broods at the

three life stages (hatch [all hatched eggshells within a nest], chick [8–12 days old], and

youth [4–6 weeks old]). All unhatched eggshells within successful nests were excluded

from relatedness calculations. Mean pairwise relatedness values between brooding adults

and their brood were averaged for each species at the three life stages. Differences

between means were calculated using simple *t*-tests.

Results

During the 2013 and 2014 breeding seasons, I collected and genotyped 223 scaled

quail eggshells (218 hatched, 5 unhatched) in 22 nests. I collected 1,149 hatched and

unhatched bobwhite eggshells from 88 successful nests. From this larger sample, 34

bobwhite nests that included 420 bobwhite eggshells (388 hatched, 32 unhatched) were

randomly selected for genotyping. Of the 420 bobwhite eggshells, 12 of these occurred

in two scaled quail nests. All scaled quail nests were incubated by females, while 25

bobwhite nests were female-incubated and nine nests were male-incubated. A total of 89

adult bobwhite and 41 adult scaled quail feathers were genotyped. Parental genotypes

were available from incubating adults for 53 clutches and for both incubating adult and

putative mate in three clutches.

Microsatellite Data Analyses

Number of alleles per locus ranged from 5 to 24 in bobwhite and 3 to 12 in scaled

quail (Table 1). PIC ranged from 0.403 to 0.919 in bobwhite and 0.504 to 0.860 in scaled

quail. Only one locus (Quail 31) exhibited a high rate of allelic drop out and was thus

excluded from further analysis. One locus (CV-P1E6) showed signs of deviations from

HWE. A high frequency of null alleles was observed in two bobwhite loci (CV-P1A7

and CV-P1E6), and three scaled quail loci (A014, A104, A022). However, these loci

were used for subsequent analyses as these deviations from HWE and high frequency of

null alleles in bobwhites were likely a direct result of the Wahlund effect (Wahlund 1928), as the two geographically distant bobwhite populations (Beaver River and Packsaddle WMA's) were analyzed as one. Additionally, high null allelic frequencies, especially in scaled quail, were likely a result of sampling and capture methodology because numerous adults were captured within potentially related social groups (coveys) in fall and winter.

Paternity Assignment

No differences in mean number of extra-pair young per nest ($P = 0.187$), mean intra-clutch pairwise relatedness ($P > 0.999$), and rates of young resulting from nest parasitism ($P = 0.450$) were observed between bobwhite populations at Beaver River and Packsaddle WMAs; therefore, these samples were combined in all subsequent analyses. Multiple paternity was identified within 29 of 34 (85.3%) bobwhite and 2 of 22 (9.1%) scaled quail nests. Within bobwhite nests, 116 of 396 (29.3%) offspring were estimated to be a result of extra-pair copulations, while 5 of 223 (2.2%) offspring from scaled quail nests were estimated to be a result of extra-pair copulations. The number of extra-pair young per nest was significantly different between the two species ($P < 0.001$); extra-pair young for bobwhites ranged from 0 to 9 (3.41 extra-pair young /nest $\pm$ 0.44 SE) and extra-pair young for scaled quail ranged from 0 to 3 (0.23 extra-pair young /nest $\pm$ 0.16 SE). Following the exclusion of young resulting from nest parasitism, the number of sires within clutches ranged from 1 to 4 (2.26 $\pm$ 0.14 SE) in bobwhite and 1 to 2 (1.09 $\pm$ 0.06 SE) within scaled quail clutches and differed ($P < 0.001$) between the two species. There was also a difference ($P < 0.001$) between the mean number of extra-pair young

per nest within female-incubated (4.28 extra-pair young/nest ± 0.48 SE) and male-incubated (1.00 extra-pair young/nest ± 0.16 SE) nests. I did not observe differences in the mean number of extra-pair young produced in the 2013 (3.05 extra-pair young/nest ± 0.54 SE) and 2014 (4.08 extra-pair young/nest ± 0.75 SE) breeding seasons for bobwhites ($P = 0.146$). Similarly, the mean numbers of young per nest were similar between 2013 (0.25 extra-pair young/nest ± 0.25 SE) and 2014 (0.21 extra-pair young/nest ± 0.21 SE) in scaled quail ($P = 0.918$). Overall, extra-pair young accounted for 25.8% and 33.3% of the bobwhite young produced in 2013 and 2014 respectively. Proportion of young resulting from extra-pair copulations did not differ between 2013 and 2014 in bobwhites ($Z = -1.621$, $P = 0.105$) or scaled quail ($Z = 0.334$, $P = 0.741$).

Nest Parasitism

Young resulting from nest parasitism were documented in 7 of 34 (20.6%) bobwhite and 2 of 22 (9.1%) scaled quail nests, which accounted for 2.9% and 5.1% of total offspring produced in bobwhite and scaled quail nests, respectively. The mean number of young per nest resulting from nest parasitism did not differ between scaled quail (0.545 ± 0.382 SE) and bobwhite (0.352 ± 0.152 SE) nests ($P = 0.643$). All young resulting from nest parasitism in bobwhite nests were a result of intraspecific nest parasitism. Within scaled quail nests, all 12 young resulting from nest parasitism were a result of interspecific nest parasitism by bobwhites. Interspecific nest parasitism was observed in two scaled quail clutches in the 2014 breeding season (Figure 1). Percentage of offspring resulting from nest parasitism was higher in 2014 (4.2% bobwhite, 7.5% scaled quail) than in 2013 (2.3% bobwhite, 0% scaled quail); however, it only differed

significantly for scaled quail ($Z = -2.498$, $P = 0.012$) and not for bobwhite ($Z = -1.082$, $P = 0.280$) clutches. There was no difference in the proportion of nests with at least one parasitic young for both species combined in 2014 (0.20) and 2013 (0.12, $Z = -0.719$, $P = 0.472$).

Alternative Reproductive Strategies

I estimated mean intra-clutch (hatched and unhatched eggshells) values of pairwise relatedness for all bobwhite (n = 34) and scaled quail (n = 22) nests that included hatched and unhatched eggshells within successful nests. The mean intra-clutch pairwise relatedness in bobwhite 0.356 (SE ± 0.004) and scaled quail 0.453 (SE ± 0.005) nests differed ($P < 0.001$). The mean intra-clutch pairwise relatedness in nests also differed between 2013 and 2014 breeding seasons for both bobwhite ($P = 0.011$) and scaled quail ($P < 0.001$) with lower relatedness occurring in 2014 than in 2013 (Figure 2).

Brood Amalgamation

To compare mean pairwise relatedness and investigate brood amalgamations, I analyzed 218 hatched eggshells within 22 scaled quail nests and 254 hatched eggshells within 24 bobwhite nests. Only hatched eggs were chosen to estimate pairwise relatedness at hatch. At the chick stage, I genotyped samples from 84 scaled quail chicks from 14 broods and 93 bobwhite chicks from 16 broods. At the youth stage, I genotyped samples from 55 scaled quail youths from 8 broods and 85 bobwhite youths from 14 broods.

I estimated that mean intra-brood pairwise relatedness at hatch was 0.372 (SE ± 0.007) for bobwhite and 0.452 (SE ± 0.006) for scaled quail and that relatedness values decreased ($P < 0.001$) from the chick to youth life stages in both species (Figure 3). A significant difference in intra-brood relatedness between the two species was observed at the hatch ($P < 0.001$) and chick ($P = 0.001$) life stages, but not at the youth life stage ($P = 0.686$).

Differences were observed in mean intra-brood relatedness between years at the hatch stage for both species ($P < 0.01$), with lower relatedness observed in 2014 than in 2013 (Table 2). Mean pairwise relatedness was similar between 2013 and 2014 at the chick stage ($P = 0.278$) and youth stage ($P = 0.100$) for bobwhites. However, differences were observed at the scaled quail chick ($P = 0.016$) and youth ($P = 0.037$) life stages (Table 2) with lower mean pairwise relatedness in 2013 than in 2014.

Discussion

Interspecific Differences in Rates of Extra-Pair Copulations

Bobwhites engaged in extra-pair copulations at significantly higher rates than scaled quail. These two similar species with similar food preferences, nesting periods, life histories, and ecologies (Schemnitz 1964) experience similar climactic and environmental conditions, yet they use significantly different reproductive strategies. Rates of extra-pair copulations observed in bobwhites were similar to rates reported with other gallinaceous species. For example, in sampled bobwhite broods, it was estimated that 10 - 20% of individuals were a result of extra-pair copulations (Faircloth 2008).

Similarly, high rates of polygamous behavior have also been observed in bobwhite and common quail (*Coturnix coturnix*) (Burger et al. 1995*b*, Rodriguez-Teijeiro et al. 2003). Rates of extra-pair copulations were significantly lower in scaled quail compared with other quail species, including sympatric bobwhites within our study area, and these interspecific differences are likely attributed to differences in population densities.

The relationship between breeding population density and rates of extra-pair copulations has been investigated in many bird species, but the connection is far from clear and many studies report contradictory results (Westneat and Sherman 1997). Several studies have shown that higher incidences of extra-pair copulations occur during higher breeding densities (Gibbs et al. 1990, Hoi and Hoi-Leitner 1997, Richardson and Burke 2001, Stewart et al. 2010, Mayer and Pasinelli 2013). In years with higher breeding densities, individuals are more likely to encounter other conspecifics, facilitating higher rates of extra-pair copulations. In our study, greater breeding densities of bobwhites may explain the higher rates of extra-pair copulations observed in bobwhites compared with scaled quail. In western Oklahoma, scaled quail occur at the far periphery of their distribution, where they are experiencing some of their lowest population densities (Sauer et al. 2014). In contrast, bobwhite populations within western Oklahoma are at the peak of their distribution-wide population densities (Sauer et al. 2014). Furthermore, according to breeding bird survey (BBS) and male call count data for our study site, bobwhites appear to have significantly higher population densities than scaled quail (Sauer et al. 2014; E. Tanner, Oklahoma State University, unpublished data). In fact, BBS results for the study area indicate that bobwhite densities may be as much as 5–10 times greater than scaled quail (Sauer et al. 2014). Given these differences in

population densities, it is probable that bobwhites encounter more conspecifics than scaled quail, thus, facilitating higher rates of extra-pair copulations.

Similar to variations in rates of extra-pair copulations, estimates of mean intra-clutch relatedness also differed between years. A difference in mean pairwise relatedness of clutches was observed between the 2013 and 2014 breeding seasons. Lower mean intra-clutch pairwise relatedness observed in 2014 occurred when relative abundance was estimated to be about 20–50% higher than in 2013, based upon male whistle count data conducted at the study sites (M. Carroll and E. Tanner, Oklahoma State University, unpublished data). While these relatedness values do not distinguish between extra-pair copulations and nest parasitism, and intraspecific differences in rates of extra-pair copulations and extra-pair young per nest were not statistically significant, the intra-clutch pairwise relatedness values do provide clear indication that individuals engaged in higher rates of extra-pair copulations and nest parasitism in 2014 than in 2013. Pairwise relatedness values did not take into account the 12 offspring that resulted from interspecific nest parasitism in the nesting season in 2014, which would make scaled quail relatedness values even lower than reported. Consequently, higher population densities in 2014 are a likely explanation for the higher rates of alternative reproductive strategies in both species.

Another factor that has been suggested to explain variation in extra-pair copulation rates among avian species is annual adult mortality rates (Griffith et al. 2002). It has been hypothesized that male abandonment of a nest as a result of high uncertainty of paternity is almost never adaptive in a species with low annual survival and thus,

males of species with short lifespans should exhibit higher rates of extra-pair copulations than males of species with long lifespans (Mauck et al. 1999). In a meta-analysis of molecular-based studies of extra-pair copulations, adult mortality explained greater than 50% of the variation in rates of extra-pair copulations, with higher rates of extra-pair copulation observed in species with lower annual survival (Wink and Dyrcz 1999, Arnold and Owens 2002). Species with few breeding seasons have limited opportunities to contribute their genes to the population, and thus, they may be more likely to engage in extra-pair copulations. While scaled quail have been shown to have slightly higher survival rates than bobwhite quail (Rollins et al. 2009; M. Carroll and E. Tanner, Oklahoma State University, unpublished data), these differences in survival are unlikely to explain variations in extra-pair copulation rates between the species.

Molecular studies investigating extra-pair copulations and nest parasitism in non-lekking gallinaceous species are sparse, however, the rates of extra-pair copulation observed in bobwhites are relatively high when compared to other socially monogamous gallinaceous species (5% for white-tailed ptarmigan [*Lagopus leucurus,* Benson 2002], 4% for willow ptarmigan [*Lagopus lagopus*, Freeland et al. 1995], and 12% for wild turkey [*Meleagris gallopavo*, Krakauer 2008]). High prevalence of extra-pair copulations observed in bobwhites may be a result of its low survival rates; annual survival probabilities of bobwhites in western Oklahoma are highly variable (0.018–0.211, Cox et al. 2004), but they are considerably lower than survival rates for many other gallinaceous species (0.44 for wild turkey [Kurzejeski and Vangilder 1987], 0.47–0.54 for willow ptarmigan [Sandercock et al. 2011], and 0.50–0.72 for white-tailed ptarmigan [Wann et al. 2014]). The low annual survival of bobwhites is likely leading to high extra-pair

copulation rates when compared with other gallinaceous species. While bobwhite and scaled quail both have low survival rates compared with most avian species, I observed high rates of extra-pair copulation in bobwhite but not in scaled quail. It appears that although differences in annual survival may be minimally contributing to variations in extra-pair copulation rates between bobwhite and scaled quail, it is also likely that survival is not the only factor contributing to the observed differences.

A third factor that has been proposed to explain variations in extra-pair copulations rates is the degree of paternal care. Rates of extra-pair copulation have been shown to be negatively correlated with levels of paternal care (Mulder et al. 1994, Griffith et al. 2002). In fact, trends in the rates of extra-pair copulations across species have been observed to decline as male contribution to care of young increases (Griffith et al. 2002). A high degree of paternal care, including nest incubation and brood rearing, is found in numerous gallinaceous species (Schemnitz 1961, Anderson 1978, Burger et al. 1995, Birks 1997, Pope 2001). During our study, about 40% of scaled quail and 60% of bobwhite chick broods had males as the primary or co-brooding adults and this high degree of paternal care makes correlations between extra-pair copulations and paternal care difficult to compare between species. Nevertheless, our results, for bobwhites seem to suggest that paternal care, primarily during incubation, may play a role in rates of extra-pair copulations.

I observed a significant difference in the mean number of young resulting from extra-pair copulations in male-incubated versus female-incubated bobwhite nests. When a male incubated a nest, significantly lower levels of extra-pair copulations were

observed within that nest. It is likely that a behavioral mechanism such as mate-guarding

occurs within these social monogamous bobwhite pairs. Although mate-guarding has not

been well documented in bobwhite or scaled quail, which is likely due to their cryptic and

secretive nature, it has been documented in Japanese quail (*Coturnix japonica*) and ring-

necked pheasant (*Phasianus colchicus*) (Nichols 1991, Ridley and Hill 2009). In a

sympatric population of black-throated bushtits (*Aegithalos concinnus*) and silver-

throated bushtits (*Aegithalos concinnus*), the proportion of nests with indications of extra-

pair copulations was lower in black-throated bushtits as these males were more likely to

incubate nests and it was hypothesized that the females were unwilling to engage in

extra-pair copulations because it may lead to reductions in male incubation and care (Li

et al. 2014). Incubation and brood rearing requires significant amounts of energy and

time while also exposing birds to increased predation risk (Burger et al. 1995*a*).

Additionally, if a male is allocating the majority of its time providing paternal care for a

brood, then he is unable to reproduce elsewhere. Therefore, it is plausible that a

bobwhite male would only incubate a nest if he is confident that a high proportion of the

offspring are his.

Intraspecific Differences in Rates of Nest Parasitism

In our study, 2.9% of bobwhite and 5.1% of scaled quail offspring were a result of

nest parasitism. These results are consistent with studies of other gallinaceous species

(2.2% for greater sage-grouse, [*Centrocercus urophasianus*, Bird et al. 2013] and 5% for

wild turkey [Krakauer 2008]). Furthermore, the percentage of nests with at least one

parasitic young was relatively consistent to other studies investigating nest parasitism in

gallinaceous species. For example, intraspecific nest parasitism was observed in 16–18%

of bobwhite nests in Florida (Faircloth 2008). Similarly, 9.6% of greater sage-grouse

nests had been parasitized (Bird et al. 2013). Although 20.6% of bobwhite and 9.1% of

scaled quail nests had at least one parasitic young, parasitic females generally contributed

only one or two eggs into another females nest. This could indicate that females are

taking advantage of periods when nests are untended, and females may be engaging in

nest parasitism in order to opportunistically increase reproductive output. Nest parasitism

may be a random occurrence that females engage in opportunistically when incidentally

encountering nests of other conspecifics.

While rates of young resulting from nest parasitism were higher in scaled quail

nests than in bobwhite nests, these results may be misleading as all of the occurrences of

nest parasitism in scaled quail nests were direct results of interspecific nest parasitism by

bobwhites. Of the 24 total offspring resulting from nest parasitism, all were a result of

parasitism by bobwhites. Interspecific differences in nest parasitism rates between

species were likely a result of differences in breeding population densities. Rates of nest

parasitism have been shown to be influenced by nesting density, with higher rates of nest

parasitism in years, species, or populations with higher nest densities (Robertson et al.

1992, Waldeck et al. 2004, Qiu-Xiang et al. 2011). Lower population densities of scaled

quail compared with bobwhites within our study area likely led to a reduced possibility of

females encountering nests of other conspecifics, limiting the opportunities for nest

parasitism.

I also observed differences between rates of nest parasitism between years. A higher percentage of young resulting from nest parasitism were observed in 2014 than in 2013, which was likely a response to higher breeding season population densities in 2014 (M. Carroll and E. Tanner, Oklahoma State University, unpublished data). In fact, I did not observe any occurrences of nest parasitism in scaled quail nests during 2013. Although differences in the percent of offspring resulting from nest parasitism between years were not statistically significant in bobwhites, they may be biologically meaningful. The higher population densities in 2014 likely facilitated increased levels of incidental contact between species, and thus higher levels of interspecific nest parasitism. Furthermore, interspecific nest parasitism was only observed during 2014 when breeding population densities were at their highest. Density is likely one of the main factors influencing nest parasitism rates between years and species.

Resource availability and nest predation have also been suggested as factors that may influence rates of nest parasitism in avian species. High nest parasitism rates have been reported in years with low resource and nest site availability (Lank et al. 1989, Valpine and Eadie 2008), or as a result of high nest predation rates (Yom-Tov 1980, Petrie and Moller 1991, McRae 1997). Nevertheless, confounding and multifaceted effects of environmental conditions on nest predation and resource availability make it difficult to test for correlations between these factors and nest parasitism rates. For example, environmental conditions such as precipitation and temperatures can have dynamic and synergistic impacts on nest survival, nesting season length, nest site availability, resource availability, reproductive output, and nest predation rates (Guthery et al. 1988, Bridges et al. 2001, Guthery et al. 2001, Hernandez et al. 2005, Lusk et al.

2006, Rader et al. 2007). However, it is likely that resources in the form of nest sites and

invertebrate food sources were not limiting. High invertebrate densities were found at

both study sites (Foye 2014, Masloski et al. 2014), and it is unlikely that food resources

in the form of invertebrates were limiting to quail populations in the study areas. Quail

are accustomed to high levels of nest predation (Schemnitz 1961, Burger et al. 1995*b*,

Lusk et al. 2006, Pleasant et al. 2006), and sometimes incubate up to three clutches a

breeding season (Cox et al. 2005). Instead of laying eggs into another female's nest,

following a predation event, it is likely that females would re-nest. I believe that resource

availability and nest predation are not influencing nest parasitism rates in quail because

habitat conditions in 2013 and 2014 were more than adequate to provide abundant

nesting sites and food resources. Population density and not nest predation or resource

availability is likely the primary factor leading to variation in nest parasitism rates

observed between scaled quail and bobwhites, along with yearly differences.

Interspecific Similarities in Brood Amalgamations

Brood amalgamations provide a number of benefits for the donating and foster

adults (Eadie et al. 1988, Lott and Mastrup 1999, Kalmbach et al. 2005, Brooks and

Rollins 2007, Lengyel 2007, Dahlgren et al. 2010), and these benefits may facilitate the

high levels of brood amalgamations observed in our study. One way that a brooding

adult can benefit from amalgamations is through brood abandonment in an effort to re-

nest. Quail experience their highest mortality rates at the beginning of their life (DeMaso

et al. 1997, Lusk et al. 2005, Pleasant et al. 2006), and brood numbers can become

depleted quickly, leaving adult quail caring for increasingly smaller broods. Through

experimental brood manipulations in Barrow's goldeneyes (*Bucephala islandica*), it was

found that brood abandonments, and thus amalgamations, increased as ducklings were

removed from the brood because a hen is more apt to abandon her brood if chick numbers

were reduced (Eadie and Lyons 1998). By abandoning one's remaining offspring into the

care of another brood, an adult can potentially re-nest (Burger et al. 1995*b*, Suchy and

Munkel 2000). Brood abandonment in an effort to re-nest has been well documented in

bobwhites (Sermon and Speake 1987, Curtis et al. 1993, Burger et al. 1995*b*, Suchy and

Munkel 2000), and these second clutches are theorized to have significant impacts on

annual production in this species (Stanford 1972, Burger et al. 1995*b*). During sample

collection and brood monitoring via radio-telemetry, I noted numerous occasions in

which brooding adults abandoned broods in addition to youth broods that were

commonly untended by a brooding adult. These unattended broods had some of the

lowest mean intra-brood relatedness values observed. It is probable that chicks within

these broods had been abandoned by a tending adult, resulting in them amalgamating into

large untended groups. Chick donation or abandonment in an effort to re-nest is likely a

primary mechanism driving the high amalgamation rates that I observed between the

chick and youth life stages in bobwhite and scaled quail.

In addition to benefiting donating adults, amalgamations can provide benefits to

both abandoned chicks and foster broods. With greater sage-grouse, it is hypothesized

that brood amalgamations allowed younger sage-grouse hens with less experience to

donate their chicks into the care of older more experienced females, thus increasing chick

survival (Dahlgren et al. 2010). In pied avocet (*Recurvirostra avosetta*), it was found that

broods that had adopted additional young had a higher chick survival rate than those that

did not. In California quail, adult members of gang broods lived longer because they spent less time being vigilant for predators and therefore, spent more time engaged in feeding and individual care (Lott and Mastrup 1999). These additional chicks and brooding adults, in communal broods work to increase vigilance as well as dilute predation risks to chicks within foster broods. Predation is often high in quail (Lusk et al. 2002, Rollins and Carroll 2001, Lusk et al. 2005) and brood rearing can expose adult to disproportionately high levels of predation risk (Burger et al. 1995*a*). Few studies have been conducted to investigate the impacts of brood amalgamations on survival in gallinaceous species; however, it is likely that due to the high predation rates experienced by bobwhite and scaled quail, amalgamations can have significant impacts on brood survival. These benefits could have led to the high rates of brood amalgamation observed in our study.

Random chance could also be a contributing factor to high rates of brood amalgamation between chick and youth life stages. During years with higher population densities, broods may come into contact on a regular basis, facilitating brood amalgamations through incidental contact. In bobwhites, it was estimated that rates of amalgamation were directly influenced by brood density and inter-brood distance across a landscape because brood amalgamations increased in years with higher population densities (Faircloth 2008). This has also been observed with surf scoters (*Melanitta perspicillata*) in which higher amalgamation rates were observed in years when brood density was highest (Savard et al. 1998). I did observe lower pairwise relatedness in 2014 than 2013 in bobwhites at all life stages; however, these differences were not statistically significant at the chick and youth life stages. Our results in scaled quail were

confounding at the chick and youth life stage, which was possibly due to small samples

sizes for scaled quail during 2013. It is possible that incidental contact may influence

rates of amalgamations, but small sample sizes and the confounding impacts of extra-pair

copulations and nest parasitism on initial brood relatedness made tests for correlations

difficult.

Although a difference in mean intra-brood pairwise relatedness from the hatch to

chick life stages was not observed within either species, significant differences were

observed from the chick to youth life stages. This indicates that brood amalgamations are

occurring frequently between the chick and youth life stages, and that both species

followed similar trends between the later life stages. Timing of amalgamations observed

is extremely important. Brood rearing is energetically costly (Pearson 1994), and the first

18 days of a quail's life are critical for thermoregulatory development (Spiers et al.

1985). Accepting additional young into a brood may only be beneficial or neutral when

individual care needs are reduced as chicks become older and more capable of caring for

themselves. As quail species rapidly grow and develop (Lusk et al. 2005), chicks become

less dependent upon a brooding adult, which increases the likelihood of brood

amalgamations and abandonment. For example, in greater sage-grouse, 70% of

amalgamations occurred with chicks between the ages of two to three weeks old

(Dahlgren et al. 2010).   After an individual reaches an age at which it can primarily take

care of itself, few drawbacks may exist for adults to adopt foster chicks into their brood.

Conclusions

Through this study of sympatric bobwhite and scaled quail, I was able to test mechanisms that lead to variations in the rates of alternative reproductive strategies across species. Significant differences observed between rates of extra-pair copulation and nest parasitism between bobwhite and scaled quail were likely a result of differences in population densities and not a result of differences in adult survival or degree of paternal care. Mean intra-clutch pairwise relatedness was lower in 2014 than in 2013 for both species, which was likely a result of increased population densities between years. Degree of paternal care did appear to impact rates of extra-pair copulations because male-incubated bobwhite nests had significantly lower extra-pair copulation rates than female-incubated nests, and rates of extra-pair copulations observed in bobwhite nests were higher than most reported estimates of extra-pair copulations in many bird species. Brood amalgamations were observed between the chick and youth life stages as chicks became increasingly mobile and independent. Although I was unable to investigate the impacts that this brooding strategy may have on brood and chick survival, I postulate that these amalgamations provide numerous benefits to both donating adults, and the foster broods that may facilitate this brooding strategy.

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Tables and Figures

Figure 1. One of two scaled quail nests parasitized by northern bobwhite females during the 2014 breeding season at Beaver River WMA in western Oklahoma (Photo by Kelsey Wellington). Northern bobwhite eggs are solid white and scaled quail eggs are white with brown flecks.

Figure 2. Mean pairwise relatedness (r) of northern bobwhite (n = 34) and scaled quail (n = 22) clutches (hatched and unhatched eggs) in 2013 and 2014 at Beaver River and Packsaddle WMAs in western Oklahoma. Values of 0.5 indicate a full-sibling relationship and 0.25 indicate a half-sibling relationship.
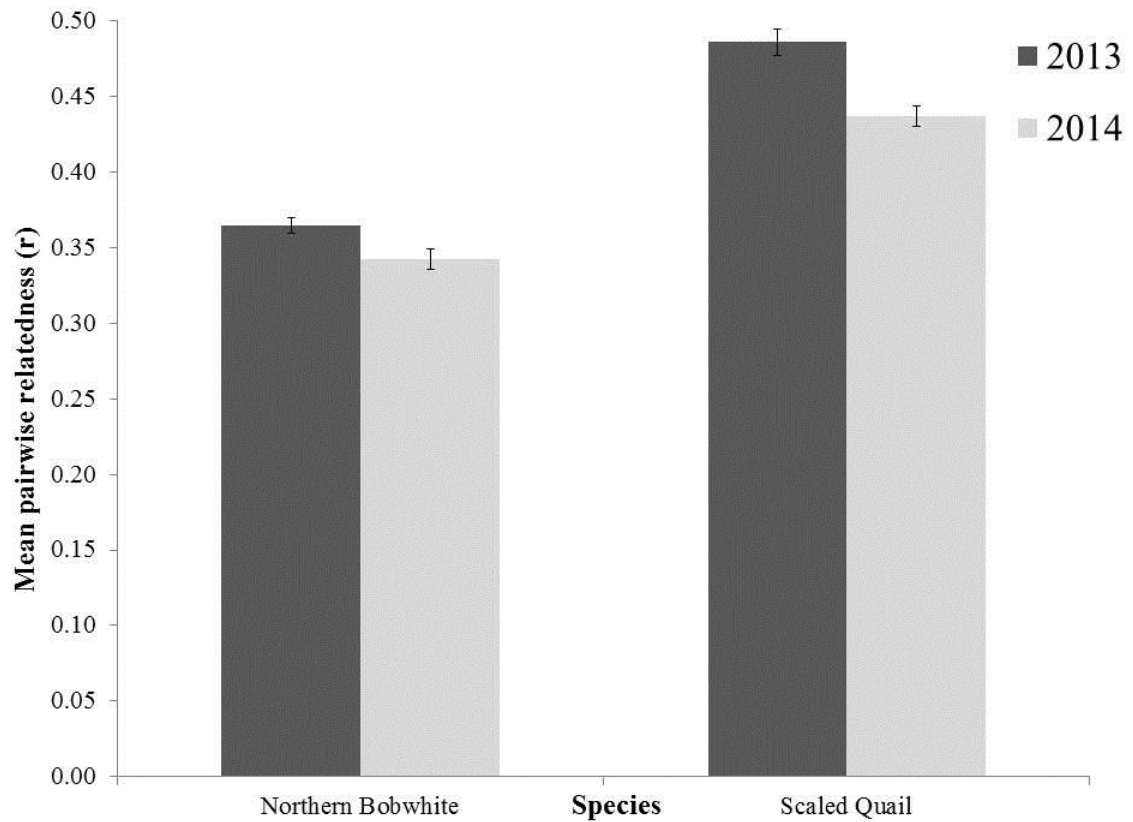
Figure 3. Mean pairwise relatedness (r) of northern bobwhite and scaled quail at three life stages (hatch [all hatched offspring], chick [8–12 days old], and youth [4–6 weeks old]) at Beaver River WMA in western Oklahoma. Samples from the 2013 and 2014 breeding seasons were pooled as one. Values of 0.5 indicate a full-sib relationship and 0.25 indicate a half-sib relationship.
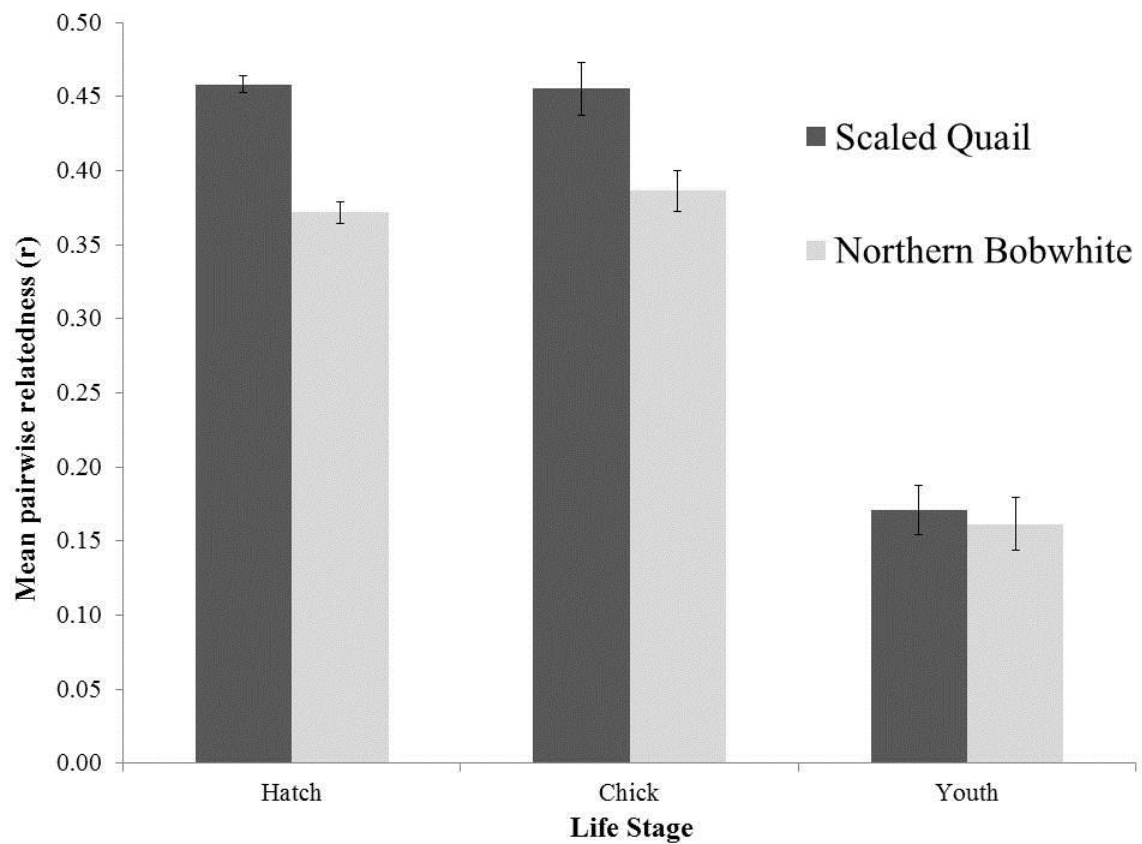
Table 1. Number of alleles (k), observed (H_o), and expected heterozygosity (H_e), and

polymorphic information content (PIC) for 89 adult northern bobwhite and 41 adult

scaled quail at Packsaddle and Beaver River WMAs in western Oklahoma during 2013

and 2014.

Species	Locus	N	k	H_o	H_e	PIC
Northern Bobwhite	Quail 3	87	24	0.851	0.929	0.919
Northern Bobwhite	Quail 44	89	5	0.449	0.442	0.403
Northern Bobwhite	Quail 13	89	20	0.820	0.893	0.878
Northern Bobwhite	Quail 30	87	16	0.874	0.892	0.877
Northern Bobwhite	Quail 22	87	12	0.908	0.889	0.873
Northern Bobwhite	Quail 23	86	15	0.884	0.889	0.873
Northern Bobwhite	CV-P1F3	86	12	0.837	0.827	0.805
Northern Bobwhite	CV-PCF5	86	15	0.837	0.898	0.884
Northern Bobwhite	CV-P1A7	85	7	0.635	0.719	0.668
Northern Bobwhite	CV-P1E6	82	10	0.463	0.770	0.736
Scaled Quail	C023	40	12	0.750	0.805	0.779
Scaled Quail	A014	36	7	0.583	0.766	0.722
Scaled Quail	A110	41	3	0.683	0.592	0.504
Scaled Quail	C015	40	7	0.725	0.679	0.645
Scaled Quail	C009	41	12	0.878	0.884	0.860
Scaled Quail	A114	39	12	0.897	0.826	0.798
Scaled Quail	A104	40	11	0.725	0.813	0.779
Scaled Quail	C022	40	8	0.800	0.783	0.742
Scaled Quail	A001	40	8	0.925	0.871	0.844
Scaled Quail	A022	34	8	0.647	0.831	0.795
Scaled Quail	B105	40	5	0.850	0.748	0.695
Scaled Quail	A018	8	8	1.000	0.883	0.807

Table 2. Mean pairwise relatedness (r) ± SE of northern bobwhite and scaled quail at 3 life stages (hatch [all hatched offspring], chick [8–12 days old], and youth [4–6 weeks old]) in 2013 and 2014 at Beaver River WMA in western Oklahoma. Values of 0.5 indicate a full-sibling relationship and 0.25 indicate a half-sibling relationship.

Life Stage	Year	Northern Bobwhite			Scaled Quail		
		# of Pairwise Comparisons	# of broods	Mean Pairwise Relatedness (± SE)	# of Pairwise Comparisons	# of broods	Mean Pairwise Relatedness (± SE)
Hatch	2013	360	11	0.398 ± 0.011	359	8	0.492 ± 0.009
	2014	452	6	0.351 ± 0.010	696	14	0.441 ± 0.007
	Pooled	812	17	0.372 ± 0.007	1055	22	0.458 ± 0.005
Chick	2013	87	8	0.407 ± 0.019	60	4	0.385 ± 0.029
	2014	160	8	0.375 ± 0.019	162	10	0.481 ± 0.022
	Pooled	247	16	0.386 ± 0.014	222	14	0.455 ± 0.018
Youth	2013	144	6	0.185 ± 0.021	58	2	0.109 ± 0.041
	2014	117	8	0.133 ± 0.023	167	6	0.193 ± 0.019
	Pooled	261	14	0.162 ± 0.016	225	8	0.171 ± 0.018

CHAPTER III

EVALUATING THE EFFICACY OF BROOD FLUSH COUNTS FOR TWO QUAIL SPECIES

Abstract

Brood flush counts are a common method used to estimate brood and chick

survival in many gallinaceous bird species. While this methodology is suitable to

investigate habitat selection and movement, survival estimates may be biased because of

low detection probabilities, brood amalgamations including brood abandonment, and

mortality of the brooding adult. In this study, I compared brood survival estimates from

radio-tagged chicks to a method that mimics the methodology of a brood flush count in a

sympatric population of northern bobwhite (*Colinus virginianus*) and scaled quail

(*Callipepla squamata*) chicks (8–12 days old) and youths (4–6 weeks old). In bobwhites,

the 3-week chick and 5-week youth period brood survival estimates were higher using

the telemetry-based estimate than the flush estimate at both the chick (0.808 vs 0.500)

and youth life stages (0.636 vs 0.364). In scaled quail, survival estimates were similar at

the chick (0.842 vs 0.789) and youth life stages (0.818 vs 0.818). With lower

occurrences of brooding adult mortality and less incidences of brood abandonment during

the chick monitoring period for scaled quail, flush counts may provide a more accurate

estimate of chick survival with this species. Biases associated with the brood flush count technique have the potential to impact population viability analysis in addition to leading to erroneous correlations between survival and environmental or individual covariates. Researchers using flush counts to investigate chick survival in gallinaceous species should work to better understand the impact that brood amalgamation, brood abandonment, and adult mortalities may have on flush count survival estimates.

Introduction

Brood flush counts are commonly used by researchers and managers as a method to investigate chick and brood survival in gallinaceous species (Palmer et al. 1998, Pleasant et al. 2006, Tirpak et al. 2008, Goddard and Dawson 2009, Musil and Connelly 2009). During a brood flush count, researchers locate radio-tagged brooding adults, either diurnally or nocturnally, and then flush the chicks on foot or in some cases with the assistance of dogs. Data collected from this methodology have been used to estimate: daily chick survival (Roberts et al. 1995, DeMaso et al. 1997, Pitman et al. 2006*a,* Pollentier et al. 2014), habitat use and movement (Haulton et al. 2003, Hagen et al. 2005), brood survival (Matthews et al. 2011, Fields et al. 2006, Pleasant et al. 2006), and impacts of radio-transmitters on survival (Hubbard et al. 1999, Manzer and Hannon 2008, Schole et al. 2011).

Although brood flush counts have been used for decades, numerous issues exist with regard to its accuracy. For example, the accurate detection of chicks within broods has been shown to differ substantially depending on the searching technique used to detect chicks (Dahlgren et al. 2010*a*). During brood flush counts, not all chicks may

flush with the brooding adult as some may run or hide in thick vegetation making accurate counts difficult. The cryptic appearance of chicks and their unique behavioral adaptations to disturbance make flush counts problematic in many gallinaceous species (Godfrey 1975, DeVos and Mueller 1993, Dahlgren et al. 2010*a*). For example, with the use of radio-tagged adults, it has been estimated that brood counts may underestimate brood numbers as much as 53% in ruffed grouse (*Bonasa umbellus,* Godfrey 1975). Additionally, Haulton (1999) observed that the vegetation and topographical features of a landscape had the potential to greatly decrease the effectiveness of flush counts. Broods within thick vegetation may be more likely to hide or run instead of flushing. While working with greater sage-grouse (*Centrocercus urophasianus*), Dahlgren et al. (2010*a*) found that flush counts may only accurately identify 72% of chicks present within a brood. These brood detection issues have the potential to significantly impact estimates of gallinaceous chick survival, which can potentially lead to erroneous correlations between survival and environmental covariates.

Some studies address the issue of low detection probabilities through the use of multiple observers, repeated verification, thorough searches, nocturnal counts, and use of observers without *a priori* knowledge of brood size (DeVos and Mueller 1993, Hubbard et al. 1999, Pitman et al. 2006*a*, Pleasant et al. 2006, Tirpak et al. 2008). Despite this, the cryptic appearances, brood amalgamations, and high mortality rates of many gallinaceous species are a concern and biases are largely unquantified for most species.

One of the primary factors that can influence survival estimates that are based upon flush counts is brood amalgamation. Amalgamations are a common brooding

strategy that has been documented in numerous gallinaceous species (Lehmann 1941, Mills and Rumble 1991, Sandercock et al. 1994, Wong et al. 2009, Guttery 2011). These amalgamations can take the form of adoptions, kidnapping, crèching, and gang-brooding (Eadie et al. 1988, Afton and Paulus 1993, Faircloth et al. 2005). Brood amalgamations can occur when: (1) chicks are adopted by a female after becoming separated from other broods or following the death of a brooding adult, (2) chicks move from one brood to another after incidental contact, (3) a brooding adult abandons chicks into the care of another brooding adult, or (4) two or more broods join together to form larger gang broods (Strong et al. 1986, Afton and Paulus 1992, Lott and Mastrup 1999, Brooks and Rollins 2007, Dahlgren et al. 2010*b*).

In addition to brood amalgamations, deaths of brooding adults can also influence survival estimates. Survival rates are often low in many gallinaceous species and reproductive activities including nesting and brood rearing expose adults to high levels of predation (Burger et al. 1995*a*, Hannon et al. 2003, Rollins et al. 2009, Manzer and Hannon 2008, Dinkins et al. 2014). When a brooding adult suffers mortality, chicks may join other broods to gain parental care (Dahlgen et al. 2010*b*). Some studies may censor broods or assume all chicks are deceased following the death of a radio-tagged adult (Roberts et al. 1995, Pollentier et al. 2014), but most studies apparently do not address this scenario.

Although issues with flush counts are often noted in studies investigating gallinaceous species, they are rarely addressed. Furthermore, a dearth of knowledge exists in regards to the accuracy of this technique in gallinaceous species. The primary

objective of this research was to investigate the bias that brood amalgamations and brooding adult mortality may have on brood and chick survival estimates generated from flush counts. I investigated the biases in a sympatric population of northern bobwhite (*Colinus virginianus;* hereafter, bobwhite) and scaled quail (*Callipepla squamata*) in western Oklahoma.

Materials and Methods

This study was conducted on Beaver River Wildlife Management Area (WMA) in western Oklahoma. Beaver River WMA is owned and managed by the Oklahoma Department of Wildlife Conservation with its primary objectives being management for upland game and other game species. The study area is approximately 11,315 ha and is characterized by sand sagebrush (*Artemisia filifolia*) and mixed grass riparian bottomlands with shortgrass uplands. The 3 dominant soil types at the WMA include Mansic Irene, Eda Tivoli, and Mobeeti-Veal-Devol-Lincoln-Eda (Carter and Gregory 1996). The average annual precipitation at the WMA is 54.61 cm with an average daytime high temperature of 35° C in July (Oklahoma Climatological Survey 2012). Throughout this study site, bobwhites and scaled quail occur sympatrically, with both species existing at the peripheries of their distributional ranges.

As part of a companion research project, bobwhite and scaled quail adults were captured and fitted with 7-g necklace-style radio-transmitters (Advance Telemetry Systems, Isanti, MN). Adults were tracked 5 days/week during the nesting season, and nests were checked daily following nest initiation. Following hatching, I tracked brooding adults daily, and an initial capture event took place when broods reached 8–12

days old (chicks). Broods were located with radio-telemetry and captured using a

combination of techniques described by Smith et al. (2003) and Andes et al. (2012)

facilitated by the use of a Thermal Imaging Camera i7® (FLIR Systems, Wilsonville,

OR). After capture, chicks were held in a collapsible cooler with a warm-water bottle to

prevent hypothermia. Chicks were fitted with 0.45 g suture style transmitters (American

Wildlife Enterprises, Monticello, FL) that had an expected battery life of 21–23 days.

The 0.45 g transmitters were attached using methods described by Burkepile et al. (2002)

and Dreitz et al. (2011).

A second capture took place when broods reached 4–6 weeks old (youths).

Broods were located using radio-telemetry and a FLIR Thermal Imaging Camera i7®

approximately 2 hours before sunrise. After a brood was located, 1 researcher

illuminated the brood using two handheld spotlights (Waypoint®, Eagleville, PA), while

a second researcher captured the brood with a 120-cm diameter hoop-net attached to a

2.25-m pole. Following capture, youths were fitted with 1.7-g expandable necklace-style

transmitters (American Wildlife Enterprises, Monticello, FL) that had an expected battery

life of 80 days. Additional youth broods were added to the study opportunistically using

Stoddard funnel traps (Stoddard 1931). These broods were aged based upon plumage

characteristics and mass at capture (Smith and Cain 1984, Lusk et al. 2005). Capture and

handling protocols were reviewed and approved by Oklahoma State University's

Institutional Animal Care and Use Committee (ACUP #AG-13-2 and ACUP #AG-11-

22).

Following capture, chick broods were tracked 6–7 days/ week and youth broods were tracked 5 days/week to estimate survival and mortality. If a marked chick was farther than 50 m from a brooding adult, chicks were flushed to determine if mortality had occurred, or if an amalgamation event had taken place. When radio-tagged chicks were no longer present with a brooding adult, broods were flushed on a weekly basis to verify presence of at least one brooding chick. If brooding adults were without chicks during the weekly daytime flush count, I conducted a nightly roost count with a FLIR Thermal Imaging Camera i7® using the methodology described by Andes et al. (2012) to verify the absence of chicks. To estimate brood survival, I used a conservative designation of a successful brood or hen as having at least one surviving chick (Fields et al. 2006, Goddard and Dawson 2009, Matthews et al. 2011, Lebeau et al. 2014, Pollentier et al. 2014).

The apparent mortality of radio-tagged chicks was estimated at the chick and youth life stages for each species. I attributed mortalities or signal losses that occurred within 3 days of transmitter attachment to be a result of transmitter failure or capture-related effects, and they were censored from analysis. Due to the small size and limited range of transmitters, signal loss was common and was likely a result of a predation event. When a chick transmitter signal was lost, I searched the area extensively within 1–2 km of the last known location, and missing birds were assumed to have suffered from mortalities. I chose to extensively search within a 2 km radius of the last known brood location because our maximum recorded daily movement was approximately 1.6 km, and it is unlikely that a chick's daily movement would exceed this distance. In the event of signal loss of a youth transmitter, individuals were censored from analysis.

For analysis, I estimated survival using two methodologies: (1) 'telemetry' or the survival of one or more radio-tagged chicks or youths within a brood (radio-tagged during a chick or youth capture event) even if that chick was no longer with the original brooding adult, and (2) 'flush' based on presence of at least one chick with a brooding adult at the end of the sampling interval. Telemetry estimates, based upon radio-tagged chicks, accommodated amalgamations in cases in which brooding adults abandoned their chicks to another adult, or when brooding adults suffered mortality and chicks moved to the care of a secondary brooding adult, or joined another brood. While broods with surviving radio-tagged chicks were not flushed, the 'flush' survival estimate based on chick presence with brooding adults, mimicked survival that would be based upon brood flush counts. Broods were flushed only when all radio-tagged chicks within the brood had died to minimize disturbance.

Period brood survival was calculated using the Kaplan-Meier product limit estimator (Kaplan and Meier 1958). I defined the day of capture as day 0 for all broods regardless of capture date. If a brood had two radio-tagged brooding adults, I only considered the brooding adult that had been the incubating adult for analysis as having 2 radio tagged adults is rare, and many survival studies include only radio-tagged females in their studies (Pleasant et al. 2006, Goddard and Dawson 2009, Lebeau et al. 2014). I used Z-tests (Pollock et al. 1989) to compare Kaplan-Meier period survival estimates between 'telemetry' and 'flush' methods for northern bobwhite and scaled quail at the chick and youth life stages. In order to avoid type II errors, alpha levels were set at 0.10.

Results

During the 2013 and 2014 seasons, I attached transmitters to 191 chicks (99 bobwhite and 92 scaled quail) within 45 broods (26 bobwhite and 19 scaled quail), and 100 youths (51 bobwhite and 49 scaled quail) within 22 broods (11 bobwhite, 11 scaled quail). Due to resource limitations and incomplete brood captures, not all of the chicks within broods were radio-tagged. Within chick broods, radio-tagged chicks accounted for 75–100% of the chicks in 28 broods, 50–75% of the chicks in 6 broods, 25–50% of the chicks in 5 broods, and 16.7–25% of the chicks in 6 broods. Within youth broods, radio-tagged chicks accounted for 75–100% of the chicks in 8 broods, 50–75% of the chicks in 7 broods, 25–50% of the chicks in 4 broods, and 12.5–25% of the youths in 3 broods. A total of 7 chicks and 16 youths were censored from the data, due to signal loss or transmitter failure. At the chick stage, apparent mortality rates were 27.8% for bobwhites and 51.7% for scaled quail, while at the youth stage apparent mortality rates were 22.5% for bobwhites and 15.9% for scaled quail.

I found that period survival estimates using the 'telemetry' estimates were higher than the 'flush' estimates at both the chick (telemetry = 0.808 ± 0.077; flush = 0.500 ± 0.098; $Z = 2.665$, $P = 0.004$) and youth life stages (telemetry = 0.636 ± 0.145; flush = 0.364 ± 0.145; $Z = 1.452$, $P = 0.0731$) in bobwhites (Table 1). For scaled quail, Kaplan-Meier period survival estimates were similar between methodologies at both the chick (telemetry = 0.842 ± 0.084; flush = 0.789 ± 0.094; $Z = 0.446$, $P = 0.328$) and youth (telemetry = 0.818 ± 0.116; flush = 0.818 ± 0.116; $Z = 0$, $P > 0.999$) life stages (Table 1). Differences in survival estimates between the 2 methodologies were attributed to brood

abandonments (n = 5, [4 bobwhite and 1 scaled quail]) leading to brood amalgamations and death of the brooding adult (n = 11, [9 bobwhite and 2 scaled quail]) in 22.7% of the youth broods and 24.4% of the chick broods. Overall brood abandonment and death of the brooding adult combined accounted for discrepancies in 23.9% of total broods.

Discussion

Brood flush counts are a common sampling methodology used to estimate chick survival in gallinaceous birds; however, recent research has begun to elucidate some of the inherent issues with this technique. Survival estimates based upon flush counts can be biased as a result of low detection probabilities (Godfrey 1975, Healy et al. 1980, Dahlgren et al. 2010*a*), high levels of brood amalgamations (Flint et al. 1995, Faircloth et al. 2005, Dahlgren et al. 2010*b*), and brooding adult mortality. Throughout our study, I observed differences between 'telemetry' and 'flush' survival estimates at the chick and youth stages in bobwhites, with the telemetry estimates being higher. In bobwhites, flush counts appear to be biasing survival estimates low. The differences between methodologies were primarily a result of brood abandonment leading to brood amalgamations and the death of brooding adults. Alternately, significant differences between sampling methodologies were not observed in scaled quail at the chick or youth life stages. It is probable that interspecific differences in brooding adult survival and frequency of brood abandonments between bobwhite and scaled quail led to differences in the accuracy of the flush count technique. With fewer brooding adults suffering from mortalities and fewer brood abandonments occurring during the monitoring period, scaled quail brood survival estimates were less likely biased than were bobwhites.

The differences observed between flush and telemetry methodologies in bobwhites are not unique to our study. With the use of radio-transmitters fitted to chicks at early life stages, differences between flush and telemetry-based survival estimates have become increasingly clear in numerous gallinaceous species (Speake 1985, Hubbard et al. 1999, Manzer and Hannon 2008). For example, Manzer and Hannon (2008) found that sharp-tailed grouse (*Tympanuchus phasianellus*) chick survival probabilities from hatch to 30 days old based upon radio-tagged chicks were significantly higher than estimates based upon flush counts (0.47 vs 0.28). Similarly, in wild turkeys (*Meleagris gallopavo*), differences between telemetry and flush count survival estimates have been observed from hatch to 28 days old ([0.52 vs 0.40], Hubbard et al. 1999), and from 1-64 days old ([35.1% vs 21.2%, percent survival] Speake et al. 1985). While not always statistically significant, these differences in chick survival estimates have the potential to severely impact population viability analysis, along with leading to erroneous correlations between survival and environmental or individual covariates.

Brood amalgamations, in the form of brood abandonment, were one of the leading causes of differences in bobwhite survival estimates between telemetry and flush methodologies. I observed radio-tagged brooding adults abandoning their broods on 5 occasions with adults leaving their chicks into the care of another brooding adult or a large gang-brood. The occurrence of brooding adults abandoning chicks in an effort to re-nest has been well documented in numerous quail species (Gullion 1956, Francis 1965, Curtis et al. 1993, Suchy and Munkel 1993), especially early in the breeding season when hens may have ample opportunity to re-nest (Sermons and Speake 1987). In Gambel's quail (*Callipepla gambelii*), it was observed that over half of all chicks were without a

brooding adult in early July, likely as a result of high levels of brood abandonment

(Gullion 1956). Using a classic flush count methodology it may be assumed, often

mistakenly, that chicks within a brood have been depredated or suffered from mortality

following brood abandonment, which will certainly bias survival estimates low.

Brood abandonment was not the only mechanism facilitating brood

amalgamations within our study area. While I was able to document the occurrence of

amalgamations resulting from adult abandonment, it was impossible to quantify the rates

of individual chick amalgamations within broods using radio-telemetry. This was due to

difficulties accounting for bi-parental care, adoptions, and communal brooding.

However, high rates of brood amalgamation have been observed in other quail

populations. For example, DeMaso et al. (1997) reported a net gain of chicks within 25%

of broods between the ages of 20-39 days old. In a similar study, Faircloth et al. (2005)

estimated brood amalgamations were observed in 55.2% of broods between ages of 10-12

days old. In California quail (*Callipepla callifornica*), communal brooding was observed

in 12% of all broods (Lott and Mastrup 1999). In addition to quail, high rates of brood

amalgamation have been observed in other gallinaceous species. For example, in greater

sage-grouse, brood amalgamations occurred in 43% of broods (Dahlgren et al. 2010*b*).

High rates of amalgamations have also been reported with wild turkey in the form of

communal brooding (38% of broods, Spears et al. 2005), and in white-tailed ptarmigan

(*Lagopus leucurus*), and rock ptarmigan (*Lagopus mutus*) populations (13%–14% of

broods, Wong et al. 2009) as a result of adoptions. Although brood amalgamations have

been observed for decades, only recently have researchers begun to understand the

prevalence of this alternative brooding strategy (DeMaso et al. 1997, Lott and Mastrup

1999, Faircloth et al. 2005, Wong et al. 2009, Dahlgren et al. 2010*b*). This strategy is not

a rare occurrence, but a common and prevalent brooding behavior documented in as

many as 23 species and subspecies of North American gallinaceous birds (Table 2). If

survival estimates are based upon the number of individual chicks within a brood, which

is standard, then results may be significantly biased as a result of brood amalgamations.

In addition to brood amalgamations, the death of the brooding adults was a

common cause of disparities in survival estimates between flush and telemetry

methodologies. Throughout the chick and youth observation periods a total of 11

brooding adults suffered from mortalities. When a brooding adult suffered mortality, the

remaining chicks either joined with another brood located in close proximity, or

alternately, primary care transferred to a secondary brooding adult that had not been

radio-tagged. The death of a brooding adult has the potential to significantly impact

survival estimates. In numerous gallinaceous species, breeding season adult survival

rates have been shown to be low (0.22–0.80 for scaled quail, [Rollins et al. 2009], 0.33

for northern bobwhites [Burger et al. 1995*a*], 0.561 for ring-necked pheasant [*Phasianus

colchicus*, Snyder 1985], and 0.68 for lesser prairie-chicken [*Tympanuchus pallidicinctus*,

Hagen et al. 2007]). Furthermore, adults are exposed to disproportionately high levels of

predation risk during reproduction and brood-rearing (Roberts et al. 1995, Hannon et al.

2003, Hagen et al. 2007, Manzer and Hannon 2008, Lyons et al. 2009, Dinkins et al.

2014).

If a brooding adult suffers mortality, chicks within the brood have not necessarily

suffered mortalities. Since precocial chicks rapidly develop, they are highly capable of

moving to another brood if the brooding adult has suffered mortality. In sage-grouse, radio-tagged chicks joined other broods within 48 hours following the death of their brooding adult (Dahlgren et al. 2010*b*). Some studies may censor broods whose adults have suffered mortalities or assume that all chicks had died following the death of a brooding adult (Roberts et al. 1995, Pollentier et al. 2014), however, a consensus does not exist throughout the literature and most studies fail to mention this scenario. In many studies utilizing flush counts, the death of a brood adult would lead to an inaccurate estimate of brood failure and chick mortality, biasing survival estimates low.

Brooding adults do not need to suffer mortalities in order for researchers to inaccurately determine that a brood has failed or that chicks have perished. In quail and socially monogamous grouse species, bi-parental care of broods is common (Schemnitz 1961, Anthony 1970, Martin and Cooke 1987, Burger 1995*b*, Delehanty 1995, Pope and Crawford 2001). It is standard protocol to attach transmitters only to hens and not to the putative father when conducting research on brood survival (Pleasant et al. 2006, Goddard and Dawson 2009, Lebeau et al. 2014). If a radio-tagged brooding hen abandoned her brood into the care of the untagged putative father, then brood and chick survival estimates would be biased low as the brood would no longer be with the radio-tagged brooding adult. Within our study, it was observed that scaled quail females abandoned their broods into the care of the putative father. While I was unable to document this conclusively as transmitters could only be fitted to chicks when they reached 7–11 days old, this likely occurred with at least 40% of the incubating adults that hatched nests throughout the 2013 and 2014 breeding seasons. This abandonment by brooding scaled quail females typically occurred early in the nesting season, when hens

63

would have ample opportunity to re-nest. This early abandonment made it impossible to estimate chick survival from hatch to initial transmitter attachment. The occurrence of brood abandonment by a female into the care of the putative fathers is not unique to scaled quail as it has been documented in the closely related California quail (Francis 1965) and Gambel's quail (Gullion 1956). Bi-parental care may influence survival estimates in socially monogamous quail and grouse species in a similar manner as the death of a brooding adult, leading to biased survival estimates, especially in the initial stages of brood rearing.

Although differences were noted in survival estimates between flush and telemetry methodologies in bobwhite broods, these differences were not observed in scaled quail. Throughout our study, the death of a brooding adult was more common in bobwhites than in scaled quail at both the chick and youth life stages. Only 2 of 11 brooding adult mortalities and 1 of 5 brood abandonments occurred with scaled quail. Genetic analysis indicated that the rates of brood amalgamations were similar between the two species (Orange 2015, Chapter 2). However, the high level of adult mortalities and higher incidences of brood abandonment observed in bobwhites resulted in greater variations in survival estimates between methodologies within this species. Annual adult survival rates of scaled quail have been reported to be slightly higher than bobwhites within the same latitude (Rollins et al. 2009). The higher survival rates of scaled quail likely reduced the impacts of brooding adult mortality on survival estimates. Furthermore, while brood abandonments were commonly observed in bobwhites during the 21-day chick monitoring period, scaled quail females were frequently documented to abandon their broods prior to the initial chick capture event. If I would have included

brood survival estimates from hatch to 7–11 days old, then our scaled quail survival estimates may have differed significantly between the 'flush' and 'telemetry' methods.

Interestingly, our estimates of brood survival using a flush count methodology would indicate that scaled quail broods have higher survival rates than do bobwhite broods, which is the opposite of what was observed with radio-tagged chicks as scaled quail chicks suffered from higher apparent mortality rates than did bobwhite quail. The high levels of brooding adult mortality and brood abandonment observed in bobwhites suggest the flush method can potentially lead to significantly biased estimates of survival within this species.

Within our study, transmitters were not attached to all chicks within each brood. As transmitters were not attached to all chicks, it is likely that the differences I observed in brood and flush survival estimates are a conservative estimate. It is probable that broods with a low proportion of the chicks radio-tagged, actually had at least one chick survive that were not radio-tagged. Additionally, while the 'flush' methodology mimics the flush count methodology; broods were not flushed on a weekly basis. By not flushing a brood with at least one surviving radio-tagged chick, an assumption of a 100% detection probability of at least one chick within a brood was made. Using a flush count technique, this assumption may be unrealistic due to the cryptic nature of gallinaceous birds; however, many studies verify that broods are without adults on multiple occasions.

A number of alternative techniques or modifications have been proposed to increase the accuracy of this technique including: dog flush counts, night roost counts, and electronic call backs or distress calls (Healy et al. 1980, DeVos and Mueller 1993,

Roberts et al. 1995, Dahlgren et al. 2010*a*, Andes et al. 2012). While these alternative methodologies may increase detection probabilities, they remain unable to account for biases in survival estimates as a result of brood amalgamations, or brooding adult mortality. The use of radio transmitters attached to chicks at a young age may provide the most accurate and least disruptive, estimates of chick survival. This method has become increasingly popular over the last decade as transmitters are being produced at increasingly smaller sizes (Manzer and Hannon 2008, Gregg and Crawford 2009, Dahlgren et al. 2010*b*, Schole et al. 2011). Although radio-tagging chicks has the potential to bias survival estimates as a result of radio-handicapping, capture related mortality, and potential transmitter detachment, survival estimates based upon radio-tagged chicks are a more direct and likely more accurate estimate of chick survival than are brood flush counts. When investigating radio-tagged chicks, researchers are not reliant upon a brooding adult and thus survival estimates are not biased as a result of adult mortality or brood abandonment. Furthermore, brood disturbance is limited using radio-transmitters as chicks would only need to be disturbed once, and not on a weekly basis.

Although researchers investigating brood survival in gallinaceous species commonly note issues with the flush count technique, this technique is still frequently used. I suggest that researchers conducting flush counts should work to investigate the impacts that brood amalgamations, brood abandonments, and brooding adult mortality may have on chick survival estimates and thus population viability analysis. Alternately, researchers should consider using miniature radio-transmitters to obtain more direct estimates of chick survival. Finally, I suggest researchers and managers should be aware

of the potential biases associated with past studies that used the flush technique and recognize the limitations of using these data.

Conclusions

While brood flush counts are useful to verify brood presence when documenting habitat use and movements, any estimates of survival using these methods are inherently biased. Brooding adults suffer from high levels of mortality, and amalgamations frequently occur as gallinaceous broods are dynamic in composition. Current knowledge based upon brood and flush counts should be viewed with caution, and researchers wishing to investigate brood and chick survival in the future, should be aware of the limitations of data collected from flush counts. The value of brood flush counts is as a relative recruitment estimate to be compared between years, sites, or treatment units, but should not be used as a means to estimate chick survival or population viability.

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Tables and Figures

Table 1. Period Kaplan-Meier brood survival (S(t) ± SE) estimates (the probability of a brood surviving the 3-week chick and 5-week youth period) for northern bobwhite (NOBO) and scaled quail (SCQU), at Beaver River WMA in western Oklahoma, 2013-2014. Survival estimates are seperated into two categories based upon sampling methodology (i.e., 'Telemetry', and 'Flush').

Age Group	Species	Interval (Weeks)	# of Broods	Telemetry S(t) ± SE	Flush S(t) ± SE
Chick	NOBO	0-3	26	0.808 ± 0.077	0.500 ± 0.098
	SCQU	0-3	19	0.842 ± 0.084	0.789 ± 0.094
	Pooled	0-3	45	0.822 ± 0.057	0.622 ± 0.072
Youth	NOBO	0-5	11	0.636 ± 0.145	0.364 ± 0.145
	SCQU	0-5	11	0.818 ± 0.116	0.818 ± 0.116
	Pooled	0-5	22	0.727 ± 0.095	0.591 ± 0.105

Table 2. North American gallinaceous bird species with documented occurrences of brood amalgamation. Brood amalgamation categories: (1) adoption, and (2) communal brooding (gang brooding and crèching). The common names of sub-species are included in parentheses.

Common Name	Scientific Name	Amalgamation	Citation
Family Odontophoridae			
California quail	*Callipepla californica*	2	Lott and Mastrup 1999
Scaled quail	*Callipepla squamata*	1	Orange 2015
Gambels quail	*Callipepla gambelii*	1	Brown et al. 1998
		2	Gullion 1956
Montezuma quail	*Cyrtonyx montezumae*	1	Wallmo 1954
Northern bobwhite	*Colinus virginianus*	1	Curtis et al. 1993
		1	Burger et al. 1995*b*
		1	DeMaso et al. 1997
		1	Faircloth et al. 2005
		2	Brooks and Rollins 2007
Family Phasianidae			
Greater prairie-chicken (Attwaters prairie-chicken)	*Tympanuchus cupido*	1	Gregg et al. 2007
	Tympanuchus cupido attwateri	1	Lehmann 1941
Lesser prairie-chicken	*Tympanuchus pallidicinctus*	1	Pitman et al. 2006*b*
Chukar	*Alectoris chukar*	2	Christensen 1970***
Greater sage-grouse	*Centrocercus urophasianus*	1	Gregg and Crawford 2009
		1	Dahlgren et al. 2010*b*
		1	Guttery 2011
Gunnison sage-grouse	*Centrocercus minimus*	1	Apa et al. 2010*
Kalij pheasant	*Lophura leucomelanos*	1, 2	Zeng 2014***
Ruffed grouse	*Bonasa umbellus*	2	Chambers and Sharp 1958
		1	Larson et al. 2001
		1	Maxson et al. 1978
Dusky Grouse	*Dendragapus obscurus*	1, 2	Wing et al. 1944**
Sooty grouse	*Dendragapus fuliginosus*	1, 2	Wing et al. 1944**
		1	Bendell 1954
Spruce grouse	*Falcipennis canadensis*	1	Keppie 1977
White-tailed Ptarmigan	*Lagopus leucurus*	1	Wong et al. 2009
Rock ptarmigan	*Lagopus mutus*	1	Wong et al. 2009

Willow ptarmigan	*Lagopus lagopus*	1	Sandercock et al. 1994
Wild turkey	*Meleagris gallopavo*		
(Eastern Wild Turkey)	*Meleagris gallopavo silvestris*	1	Hubbard et al. 1999
(Rio Grande Turkey)	*Meleagris gallopavo intermedia*	1	Metz et al. 2006
		2	Spears et al. 2005
(Merriams Wild Turkey)	*Meleagris gallopavo merriami*	1	Mills and Rumble 1991
Ocellated turkey	*Meleagris ocellata*	2	Gonzalez et al. 1998

*Experimenter manipulated, captive breeding and wild brood augmentation study

**Dusky and sooty grouse pooled as blue grouse

***Species introduced to North America

CHAPTER IV

SURVIVAL AND HABITAT USE OF NORTHERN BOBWHITE AND SCALED QUAIL

CHICKS IN WESTERN OKLAHOMA

Abstract

Northern bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*)

are experiencing long-term and range-wide population declines. To address population

declines, it is important to have a thorough understanding of the brooding behavior and

survival of these species. Quail experience their highest mortality rates in the beginning

stages of their life, and the vegetation communities utilized throughout brood rearing

period may have significant impacts on chick survival. The objective of this study was to

investigate and compare the habitat use, movement, and survival of two sympatric quail

species existing at the periphery of their distributional ranges. The comparison of

sympatric and closely-related species provides us with an opportunity to better

understand the mechanisms that may limit population growth and recruitment.

Throughout this study, broods were tracked from 0–80 days old to investigate habitat use

and movement patterns of both species. To investigate survival, chicks also were

captured twice in this study and fitted with radio-transmitters at 2 life stages (chick [8–12 days old] and youth ([4–6 weeks old]). Throughout the 2013 and 2014 breeding seasons, radio-transmitters were attached to 196 chicks (102 bobwhite, 94 scaled quail) and 153 youths (94 bobwhite, 59 scaled quail). Scaled quail exhibited greater daily movements than northern bobwhites throughout the brood-rearing periods. Significant interspecific differences were observed in habitat selection with bobwhites selecting mixed-shrub and sand-sagebrush vegetation communities. I also found that northern bobwhites utilized areas with greater visual obstruction and overhead cover during times of thermal extremes, whereas scaled quail did not. The 20-day survival probability for chicks was higher in bobwhites (0.725 ± 0.068) than in scaled quail (0.488 ± 0.085), while the 35-day survival probability for youths was similar between bobwhite (0.788 ± 0.086) and scaled quail (0.795 ± 0.110). The levels of habitat partitioning observed across the study area, likely had dynamic and multifaceted effects on chick and youth survival. Results from this project will assist researchers with a better understand of various aspects of quail ecology, which will enable managers to more effectively manage these sympatric quail populations.

Introduction

Throughout their distributional ranges, northern bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) are experiencing severe and long-term population declines (Brennan 1991, Hernandez et al. 2013, Sauer et al. 2014). These population declines have been attributed to a wide range of factors such as land use change, habitat fragmentation, improper grazing, urbanization, and the exclusion of natural processes including fire (Brennan 1991, Schemnitz 1993, Hernandez et al. 2013). As r-selected species, nesting and brood rearing are

vital periods during the life history of quail and can significantly impact recruitment. Although

numerous studies have been implemented to investigate the survival of northern bobwhite

chicks, and to a significantly lesser extent, scaled quail chicks, much is still unknown about this

ecologically critical life stage. Furthermore, much of the current knowledge of chick survival is

based heavily on results from brood flush or nightly roost count methodologies (DeMaso et al.

1997, Suchy and Munkel 2000), which have a number of inherent flaws. Survival estimates

based upon flush counts in gallinaceous species are likely biased as a result of inherent issues

with this technique, including brood mixing, low detection probabilities, and brooding adult

mortality (Godfrey 1975, Healy 1980, Faircloth et al. 2005, Dahlgren et al. 2010*a,* Dahlgren et

al. 2010*b*). The use of miniature radio-transmitters, attached at a young age, has the potential to

increase the accuracy of survival estimates by providing a more direct measure of chick survival.

It is important to have a comprehensive knowledge of a species' habitat preference,

especially during the initial stages of their life when they may be most vulnerable to predation.

After hatching, chicks will quickly leave the nest, where they will enter into contact with their

environment while at the same time experiencing the highest mortality rates of their lives

(DeMaso et al. 1997, Lusk et al. 2005). The vegetative characteristics of a landscape can have

dynamic and multifaceted effects on resource availability, chick survival and brood ecology

(Madison et al. 1995). Past research has elucidated some of the important characteristics of a

landscape to brooding adults including high levels of visual obstruction to protect against

predation, high abundance of forbs and grasses to promote high invertebrate densities, and

adequate bare ground to facilitate movement and feeding (DeVos and Mueller 1993, Taylor et al

1999, Collins et al. 2009, Doxon and Carroll 2010). Additionally, habitat preferences can vary

throughout the day as birds seek thermal refuge from high operative temperatures (Forrester

1998, Taylor and Guthery 1994). While there have been many studies investigating adult

northern bobwhite ecology over the last 70–80 years, there is limited knowledge regarding the

habitat use, movement, and survival of northern bobwhite broods and chicks. Furthermore, little

information exists in regards to the habitat use and resource requirements of scaled quail broods

in the initial stages of their life.

Throughout western Oklahoma, bobwhites are existing at some of their greatest

distribution-wide densities (Sauer et al. 2014). As these bobwhite populations are located at the

periphery of their distribution, it is likely that they may be vulnerable to unfavorable

environmental conditions and potential climactic shifts facilitating the need for increased

understanding of these unique and economically important game bird species. The zone of

sympatry between these two species also provides a unique opportunity to further understand the

ecology of these species. Studying the variability in nesting and brooding survival rates of

sympatric and closely related species has been proposed as a method to better understand the

mechanisms that may limit population growth and recruitment within a species (Sieving 1992,

Koons and Rotella 2003, Ackerman et al. 2014). Therefore, the objective of this study was to

investigate and compare chick survival, habitat use, and movement of two sympatric quail

species from broad scale habitat use and movement to micro-scale habitat use, and to investigate

differences in habitat use throughout the day.

Materials and Methods

<u>Study Area</u>

This study was conducted at the Beaver River Wildlife Management Area (WMA) in western Oklahoma. Beaver River WMA (11,315 ha) is owned and managed by the Oklahoma Department of Wildlife Conservation. The average annual precipitation at the study site is 54.61 cm with the majority of rainfall occurring during spring and summer. The climate is semiarid with average maximum and minimum summer temperatures ranging between 16–35° C (Oklahoma Climatological Survey 2012).

Vegetation at Beaver WMA occurs within 3 distinct vegetation zones: riparian, mixed shrub/mixed grass, and shortgrass upland. The riparian zone is characterized by exotic salt cedar (*Tamarix* spp.) and dense stands of weeping lovegrass (*Eragrostis curvula*). The mixed shrub/mixed grass zone is characterized by sand sagebrush (*Artemisia tridentate*) that is intermixed with grasses such as switch grass (*Panicum virgatum*), Indian grass (*Sorghastrum nutans*), big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and giant sandreed (*Calamovilfa gigantea*), and other shrubs such as sand plum (*Prunus angustifolia*) and fragrant sumac (*Rhus trilobata*). The upland zone is characterized by several shortgrass species such as buffalo grass (*Buchloe dactyloides*), little barley (*Hordeum pusilium*), blue grama grass (*Bouteloua gracilis*), and cheatgrass (*Bromus tectorum*) interspersed with patches of sand plum, yucca (*Yucca glauca*), and fragrant sumac.

<u>Radio-telemetry</u>

I studied northern bobwhite and scaled quail chick survival and habitat-use during the 2012–2014 breeding seasons. Northern bobwhite and scaled quail adults were fitted with 7-g necklace style radio-transmitters (Advanced Telemetry Solutions, Isanti, MN), and nests were located via telemetry and checked daily. After hatching, broods were monitored daily via the radio-marked adult until the chicks reached ages 8–12 days when the chicks were captured for attachment of radio-transmitters. I used a combination of methods described by Smith et al. (2003) and Andes et al. (2012) to capture chicks. Chicks were captured using a corral constructed around the brood while the brood was roosting. At sunrise, the brooding adult was flushed from the brood, and all chicks were captured with the use of a Thermal Imaging Camera i7® (FLIR Systems, Wilsonville, OR). Following capture, chicks were held in a small portable cooler with a warm water bottle to prevent hypothermia. Chicks were fitted with 0.45-g suture-style transmitters with an expected battery life of 21–23 days (American Wildlife Enterprises, Monticello, FL). Transmitters were attached using methods described by Burkepile et al. (2002) and Dreitz et al. (2011).

Chicks were recaptured when they reached an age of 4–6 weeks (hereafter, youths). For capture, broods were located approximately 2 hours before sunrise using radio-telemetry and a FLIR Thermal Imaging Camera i7® (FLIR Systems, Wilsonville, OR, USA). After a brood was located, one researcher spotlighted the brood with 2 handheld spotlights, while a second researcher lowered a 120 cm diameter hoop net attached to a 2.25-m pole over the roosting brood. Following capture, youths were fitted with either a 1.7-g expandable elastic necklace (American Wildlife Enterprises, Monticello, FL, USA), or a 1-g suture style (Advance Telemetry Systems, Isanti, MN) transmitter with expected battery lives between 51–81 days. Additional youths were added opportunistically using Stoddard funnel traps (Stoddard 1931). I determined

the ages of these birds based on mass and feather development (Smith and Cain 1984, Lusk et al. 2005). I fitted expandable elastic transmitters to approximately three-fourths of the youths within a brood while the rest were fitted with suture style transmitters. Suture transmitters were attached with similar protocols used for the chick stage. Attachment and capture protocols were approved by Oklahoma State University's Institutional Animal Care and Use Committee (ACUP #AG132 and ACUP #AG11-22).

Following hatching, broods were located 6–7 days/week for chicks (0–30 days old) and 5 days/week for youths (31–80 days old). I located broods by homing to a distance of 20–30 m to avoid disturbing broods. The azimuth and estimated distance to the brood location were recorded along with the coordinates of the location of the observer which were recorded with a handheld Garmin® GPSMAP® 62s (Garmin International, Inc., Olathe, KS). If all radio-marked chicks or youths within a brood had suffered mortality, broods were flushed on a weekly basis to verify the presence of at least one chick with a brooding adult in order to estimate habitat use and movement. I alternated daily telemetry locations between 2 time periods (active [sunrise–1100 and 1601–sunset] and loafing [1101–1600]) to minimize the effect of variations in diurnal habitat selection that may influence habitat analysis (Taylor and Guthery 1994, Taylor et al. 1999). When radio-tagged individuals were located at a distance > 100 m from the brooding adult, I checked chicks for potential mortalities. I classified cause of mortality into 4 categories: mammalian predation, avian predation, natural causes, and unknown. Identification of predation was based upon bite or beak marks on transmitters, location of the mortality event, evidence of predator scat or sign, and body part condition. I classified the cause of mortality as natural if trauma to the body was not evident and signs of predation were not observed. Because of the small size of chicks, predators can easily move radio-tagged individuals following a predation

event. Therefore, in the event of transmitter signal loss, I searched the area extensively within 1–2 km to locate missing individuals and individuals not located were considered a mortality. I chose to extensively search within a radius of 2 km of the last known brood location because our maximum recorded daily movement for broods was approximately 1.6 km, and it is unlikely that a chick's daily movement would exceed this distance. In the event of youth transmitter signal loss, individuals were censored on the last day known alive.

Survival Analysis

I used the Kaplan-Meier survival function (Kaplan and Meier 1958) to determine survival of chicks over a 20-day period and youths over a 35-day period. The day of marking was designated time = 0 for all chicks regardless of capture date. I attributed mortalities or signal losses that occurred within three days of transmitter attachment to be caused by transmitter failure or capture-related effects, and they were censored from survival analysis. Any chicks and youths with unknown fates resulting from radio signal loss were censored on the last day that they were known to be alive. I chose to monitor youth survival for a 35 day period and not until broods reached an age of 80 days because the high mobility of chicks and increased independence from the brooding adult as the chicks aged made telemetry difficult.

Multiple chicks were marked within most broods, and while this will not bias survival estimates, variance estimates may be biased as a result of intra-brood dependence (Flint et al. 1995). Therefore, I used the method described by Flint et al. (1995) to estimate the standard error of chick survival estimates using a bootstrap re-sampling procedure with 2,000 replicates. Survival values were reported for each species for each year along with a total survival with combined years. I compared 20-day chick and 35-day youth period survival rates between

89

species and years using a Z-test described by Pollock et al. (1989). Additionally, I compared

survival estimates between the suture and elastic necklace style transmitters at the youth stage.

All tests were considered significant at $\alpha < 0.05$.

Vegetation Measurements

A hierarchical approach was used to examine brood habitat selection at a broad-scale and

micro-scale level. I used an unsupervised max combined vegetation classification to develop a

vegetation map from 2-m resolution satellite imagery collected in July 2013 using ArcMap 10.1

(Environmental Systems Research Institute, Redlands, CA, USA) with 65 classes. From the

initial classification, I reclassified the map into 10 ecologically meaningful classes (Table 1)

using extensive first-hand knowledge of the area, along with 214 ground-truthed points.

For home range size and movement analysis, broods were segregated into categories

based on age (0–30 days old and 31–80 days old). While survival estimates for youths were

estimated over a 35 day youth period, broods were monitored to an age of approximately 80 days

old as this was the time that broods commonly began to break up and disperse. Home ranges

were calculated for broods with ≥ 20 locations (DeVos and Mueller 1993, Taylor et al. 1999).

Home range size was estimated using the Minimum Convex Polygons tool within ArcMap 10.1.

Daily brood movement was estimated as the Euclidian distance between 2 subsequent days'

locations. The percent cover of dominant vegetation communities within convex polygons was

calculated using ArcMap 10.1. All means are presented ± SE and two-sample *t*-tests or Welch's

t-test (Welch 1947), when variances were unequal, were used to investigate interspecific

differences in average home range size and movement along with differences between life

stages. Similarly, two-sample *t*-tests, or Welch's t-test were used to compare interspecific

differences in percent vegetation composition of dominant vegetation types within home ranges. All tests were considered significant at $\alpha < 0.05$.

To evaluate vegetation characteristics at brood locations, I measured visual obstruction, vegetation cover, and canopy cover of shrubs. At brood locations, I measured vegetation characteristics similar to methods described by Taylor et al. (1999) and Collins et al. (2009). Measurements were recorded at every fourth brood location, when possible. I quantified visual obstruction using a 1.2 m high and 6.5 cm wide profile board consisting of 12 10-cm alternating black and white intervals (Nudds 1977). I recorded the proportion of vegetation covering each interval while observing the board from a distance of 10 m and a height of 1.5 m from the 4 cardinal directions and from one random direction. Visual obstruction estimates were recorded in 6 classes: (1) 0–5%, (2) 5–25%, (3) 25–50%, (4) 51–75%, (5) 75–95%, and (6) 95–100%). For analysis, each class was assigned the midpoint of the cover class and I averaged the five visual obstruction estimates per point to create a single value per strata for each brood location.

The line intercept technique (Canfield 1941) was used to measure percent canopy coverage of shrubs along 4-m transects radiating from the brood location and the 4 cardinal directions. Shrub patches were considered discrete patches if canopy breaks were greater than 10 cm. I used a modified 50 x 50 cm Daubenmire frame (Daubenmire 1959) to estimate ground cover in 6 cover classes (1: 0–5%, 2: 5–25%, 3: 25–50%, 4: 51–75%, 5: 75–95%, and 6: 95–100%) for each functional group (i.e., grass, forb, legume, litter, and bare ground). Ground cover measurements were recorded at the brood location and in each cardinal direction at a distance of 4 m from the centroid of the brood location (Taylor et al. 1999). For analysis, each

class was assigned the midpoint of the cover class and I averaged the five ground cover estimates per point to create a single value for each functional group at each brood location.

I also measured angle of obstruction at each point using a protocol developed by Kopp et al (1998) as a method to quantify habitat structure. Angle of obstruction was measured using a electronic level attached to a 2-m pole. The angle of obstruction provides a single index of habitat structure with higher values indicating a more structurally dense location. I measured the angle at which the pole touches vegetation at the plot center and in the 4 cardinal directions. Measurements were recorded at the centroid of the brood location and at a distance of 4-m in each cardinal direction. The five angles of obstruction per point were averaged for each brood location.

Vegetation Analysis

I averaged visual obstruction, vegetation cover, percent canopy cover of shrubs, and angle of obstruction at brood locations for each species at active and loafing time periods and compared using a two-sample t-test, or Welch's t-test. All tests were considered significant at $\alpha <$ 0.05.

Results

Survival of Chick and Youth Life Stages

I collected data from 102 radio-marked bobwhite and 94 scaled quail chicks in addition to 94 radio-marked bobwhite and 59 scaled quail youths during the study. I radio-tagged individuals within 46 chick broods (25 bobwhite and 21 scaled quail broods), and 32 youth broods (20 bobwhite and 12 scaled quail broods). Of the 153 radio-tagged youths, 39 were fitted

with suture transmitters, and 114 were fitted with elastic transmitters. I censored 10 chicks (5 bobwhite and 5 scaled quail) and 36 youths (28 bobwhite and 8 scaled quail) from the data set due to radio-signal loss, or potential transmitter detachment. I confirmed mortalities of 72 chicks (27 bobwhite and 45 scaled quail) and 29 youths (18 bobwhite and 11 scaled quail) during the study. Due to the small size and limited signal strength of transmitters, I was unable to estimate cause specific mortality of 79.5% of chick mortalities. The remaining mortalities were due to mammalian (11.0%) and avian (9.6%) predation. At the youth life stage, 53.3% of mortalities were due to unknown causes, 36.7% from mammalian predation, 6.7% from avian predation, and 3.3% from natural causes such as exposure.

At the youth stage, 35-day period survival estimates were similar between the elastic and suture style transmitters ($Z = -1.546$, $P = 0.122$), therefore, the data were pooled for all subsequent analyses. Overall, survival rates of bobwhite chicks were significantly greater than scaled quail chicks during the study, but survival rates of bobwhite and scaled quail youths were similar during the study (Table 2). A significant difference was observed between period survival rates in 2013 but not in 2014 at the chick stage. At the youth life stage, survival rates were similar between the species. Period survival rates for bobwhite chicks were higher in bobwhites in 2014 than in 2013 at the chick stage ($Z = -2.113$, $P = 0.033$), but differences between years were not observed at the youth life stage ($Z = -0.780$, $P = 0.435$). A significant difference was not observed between years for scaled quail at either the chick ($Z = 0.153$, $P = 0.879$) or youth life stages ($Z = 0.222$, $P = 0.824$).

Daily Movement

Scaled quail had significantly greater average daily movements than bobwhites at both the chick ($t = 3.334$, $df = 1096$, $P < 0.001$) and youth life stages ($t = 8.534$, $df = 479$, $P < 0.001$). For bobwhites, average daily movements were similar between the chick (179.07 m ± 6.92, n = 670) and youth (171.74 m ± 6.63, n = 395) life stages ($t = 0.781$, $df = 996$, $P = 0.422$), but scaled quail youths (304.87 m ± 14.12, n = 336) had greater daily movements than chicks (214.70 m ± 8.38, n = 429) ($t = 5.491$, $df = 559$, $P < 0.001$). Daily movements were not compared between years as a result of small or unequal samples sizes.

During the 2012–2014 breeding seasons, I estimated home range sizes for 80 broods including 50 chick (29 bobwhite and 21 scaled quail) and 30 youth broods (18 bobwhite and 12 scaled quail) (Table 3). Scaled quail had significantly larger home range sizes when compared to bobwhites at the youth stage but not at the chick life stage (Table 3). Home range sizes for scaled quail youths were significantly greater than scaled quail chicks ($t = 2.206$, $df = 14$, $P = 0.045$), but the home ranges sizes of both life stages were similar between bobwhites ($t = 1.371$, $df = 45$, $P = 0.177$). Home range sizes were not compared between years as a result of small and unequal samples sizes.

Broad-scale Habitat Use

I use a hierarchical approach to investigate the habitat use and selection in northern bobwhite and scaled quail. I did this by investigating broad-scaled habitat selection as represented by the percentage of home ranges covered by primary vegetation types. Within home ranges, the dominant vegetation types differed between bobwhite and scaled quail at both

the chick and youth life stages (Table 3). The percentage of home ranges covered by mixed-shrub and sand sagebrush vegetation types was greater in bobwhite home ranges than in scaled quail home ranges at both the chick and youth life stages. In contrast, the percentage of home ranges covered in shortgrass/yucca was greater in scaled quail than in bobwhites at both life stages (chick, $t = 3.355$, $df = 24$, $P = 0.002$; youth, $t = 3.150$, $df = 14$, $P = 0.007$).

Micro-scale Habitat Use

I sampled micro-habitat vegetation at 293 brood locations (136 bobwhite and 157 scaled quail brood locations) in June–August during the study. Three of the micro-habitat variables (percent shrub cover, percent forb cover, and angle of obstruction) were significantly different between active and loafing periods for bobwhite broods, while none of the microhabitat variables were significantly different between active and loafing periods for scaled quail broods (Table 4). During the loafing period, bobwhite locations contained higher percent shrub cover and angle obstruction values than during the active period, but bobwhite locations contained higher percent forb cover during the active period than during the loafing period. Percent mixed-shrub cover was greater at bobwhite brood locations than at scaled quail brood locations during both active ($t = 3.803$, $df = 164$, $P < 0.001$) and loafing ($t = 4.814$, $df = 69$, $P < 0.001$) periods. Higher angle of obstruction values were observed in bobwhite than in scaled quail locations at both time periods (active, $t = 4.550$, $df = 176$, $P < 0.001$; loafing, $t = 4.209$, $df = 103$, $P < 0.001$). Scaled quail brood locations contained higher percent bare ground than bobwhite brood locations during both periods (active, $t = 4.229$, $df = 183$, $P < 0.001$; loafing, $t = 2.800$, $df = 103$, $P < 0.001$).

Significant differences were observed in an examination of differences in the visual cover profiles between active and loafing locations. For bobwhites, significant differences occurred at

stratums 5–12, while for scaled quail, differences occurred at stratums 5, 6, 9, 10, and 11 (Table 5). Significant differences were also observed in visual obstruction estimates between the two species for all stratums at both active and loafing periods ($P < 0.01$).

Discussion

With a distribution primarily within the dry and arid regions of North America, scaled quail are ecologically adapted to xeric and structurally open vegetation communities (Schemnitz 1961, Schemnitz 1964). Alternately, with a distribution predominantly in the eastern United States, bobwhites are ecologically adapted to more mesic and structurally dense vegetation communities. These general trends in ecological adaption and habitat preferences were observed within our sympatric population of bobwhite and scaled quail. Bobwhite broods primarily utilized the mesic and structurally dense mixed shrub/mixed grass vegetation zone, while scaled quail broods were primarily found within the xeric and more structurally open shortgrass upland vegetation zone within the study area. High levels of habitat partitioning appear to be occurring between the two species within the study site and these observed differences in habitat selection are likely resulting in interspecific differences in home range size, daily movement, and chick survival.

Brood Habitat Selection

Within my study site, the home ranges of scaled quail broods had significantly lower percent coverage of both mixed shrubs and sand sagebrush than did the home ranges of bobwhite broods. Moreover, I observed significant differences in the percent coverage of the

shortgrass/yucca vegetation type between species with scaled quail having more of the shortgrass/yucca vegetation type within their home ranges. For bobwhites, mixed shrubs such as sand plum, fragrant sumac, and sand sagebrush have been documented to provide a number of ecological benefits including providing loafing cover during thermal extremes, and escape cover from predation (Johnson and Guthery 1988, Guthery 2000, Guthery et al. 2005, Hernandez and Guthery 2012). While there has been little research on the requirements of mixed shrub cover for thermal or predator protection in scaled quail, it is likely that as a species adapted to arid environments (Henderson 1971), they may not utilize mixed shrubs vegetation communities to the same extent as do bobwhites as shrubs would likely be less available in arid regions. For scaled quail, a higher proportion of home ranges were covered with shortgrass/yucca vegetation community which is more commonly found throughout their distribution. Although these two species inhabit the same study site, high levels of habitat partitioning appears to be occurring as significant differences were observed in the dominant vegetation types found within their home ranges.

The observed levels of habitat partitioning and variations in resource selection observed in my study are not unique to the sympatric populations of bobwhite and scaled. For instance, in gallinaceous birds, habitat partitioning has been documented in a number of sympatric species including sympatric greater sage-grouse (*Centrocercus urophasianus*) and Columbian sharp-tailed grouse (*Tympanuchis phasianellus columbianus*) in Idaho (Apa 1998), and greater prairie-chicken (*Tympanuchus cupido*) and sharp-tailed grouse (*Tympanuchus phasianellus*) broods in South Dakota (Norton et al. 2010). In quail, differences in habitat selection between species has also been observed in sympatric populations of Gambel's quail (*Callipepla gambelii*), scaled quail (*Callipepla squamata pallida*), and masked bobwhite (*Colinus virginianus ridgwayi*)

(Guthery et al. 2001). Habitat partitioning appears to be quite common in sympatric populations of bobwhite and scaled quail at Beaver WMA, allowing both species to co-exist within a landscape by filling alternative niches.

In addition to differences in broad-scale habitat selection, there were significant interspecific differences in average home range size and daily movement between the two species. Scaled quail exhibited larger home ranges at the youth life stage and greater daily movements than bobwhites throughout brood rearing, and these differences may be a result of variations in resource abundance within the different vegetation types the broods were utilizing. Resources, including invertebrates, are an important food source for brooding bobwhite adults and their rapidly developing offspring (DeVos and Mueller 1993, Doxon and Carroll 2010). Northern bobwhite brood home range sizes have been shown to be inversely correlated with invertebrate abundance (DeVos and Mueller 1993). Similarly, willow grouse (*Lagopus lagopus*), brood movements were found to be smaller in resource rich areas with high invertebrate abundance than in poorer quality areas (Erikstad 1985). While bobwhites are primarily selecting vegetation communities within the mixed shrub/mixed grass transitional zone, scaled quail are utilizing the less structurally dense shortgrass upland zone that contains a higher proportion of bare ground. This upland zone has been documented as having lower abundances of arthropods than the riparian and transitional zones (Foye 2012). Furthermore, differences in grass, forb, and litter cover found between vegetative zones can lead to significant variations in invertebrate species composition and relative abundance. Within my study area, Masloski et al. (2014) observed significant differences in the species composition of grasshoppers between the upland and riparian vegetation zones. It is likely that the larger home ranges and greater movements observed in scaled quail as compared to bobwhites is a response

to differences in abundance and variations in invertebrate species composition within the vegetation communities that they utilize. Within areas of relatively lower invertebrate abundance, scaled quail may need to move greater distances in order to meet daily energetic demands.

An additional factor that may have facilitated differences in movement patterns and home range size is the availability of bare ground within the vegetation communities utilized by each species. Within my study area, the amount of bare ground was greater for scaled quail locations than bobwhite locations. Bare ground is important to brood-rearing adults and their chicks as bare ground allows chicks to efficiently move across a landscape (Taylor et al 1999, Collins et al. 2009). Some management recommendations for bobwhites suggest that bobwhite brooding sites should have about 50% bare ground in order to facilitate optimal feeding and movement (DeVos and Mueller 1993). In Kansas, it was found that diurnal bobwhite brood sites had approximately twice as much bare ground and forb cover than random points within the landscape (Taylor et al. 1999). Higher proportions of bare ground found at scaled quail brood sites as compared to bobwhite brood sites may have facilitated the observed differences between species. With higher proportions of bare ground cover at active and loafing brood locations, scaled quail chicks are likely able to more rapidly and efficiently move throughout the landscape.

Interestingly, home range and daily movement estimates increased significantly from the chick to youth life stages in scaled quail, but they did not increase for bobwhites. This difference between the two species may also be explained by differences in resource abundance within the vegetation communities utilized by each species. In ruffed grouse (*Bonasa umbellus*), it has been observed that adult home range sizes were more than twice the size in years with high food

99

resource abundance as compared to years with low resource abundance (Whitaker et al. 2007).

Within my study site, scaled quail may need to increase their home range size and daily

movements as they develop in order to fulfill increased energetic demands. Alternately,

bobwhites may not need to expand their home ranges in order to meet energetic demands as their

broods were primarily utilizing more structurally dense and resource rich brooding territories.

Resource abundance within bobwhite chick home ranges may be adequate to fulfill energetic

demands throughout the brood-rearing phase.

Interspecific differences in habitat selection between bobwhite and scaled quail were not

only observed at a broad-scale level, but also observed at micro-scale level. In bobwhites,

habitat preferences have been shown to vary throughout the day with broods seeking areas with

an abundance of forb and bare ground cover in the morning for feeding and dense more shaded

shrub patches for loafing during the hotter potions of the day (Johnson and Guthery 1988,

Forrester 1998, Taylor and Guthery 1994, Guthery et al. 2005). Operative temperatures of 39° C

can lead to hyperthermia in bobwhite adults (Forrester et al. 1998, Guthery et al. 2005). During

the warmer portions of the day, large portions of a landscape may become unsuitable due to high

operative temperatures (Forrester et al. 1998, Guthery et al. 2005). Consequently, during the

warmer periods of the day observed during my study, brooding bobwhites selected vegetation

communities with a higher percentage of mixed-shrub and woody cover, greater angle of

obstruction values, and higher visual obstruction that likely provide more thermal cover from the

high temperatures.

Scaled quail did not appear to be seeking thermal refuge to the same degree as bobwhites

during the warmer portions of the day. Significant differences were not observed in angle of

obstruction and percent shrub cover between active and loafing brood locations in scaled quail. While little is known about scaled quail brood habitat selection, it is probable that as they are more adapted to arid regions, and thus, more acclimated to high operative temperatures (Henderson 1971). Therefore, they may not need to seek out thermal refuge to the same degree as bobwhites. Within scaled quail home ranges, mixed shrubs such as sand sagebrush, yucca, and fragrant sumac are still common, however, less abundant. It is likely that, when necessary, scaled quail are capable of finding thermal refuge in the less common and less structurally dense mixed-shrub or sand sagebrush vegetation communities.

Survival of Chick and Youth Life Stages

Gallinaceous chicks face their highest mortality rates in the initial life stages, and the vegetation communities utilized by these species may have significant effects on survival and recruitment. I observed significant differences in survival between scaled quail and bobwhites during the chick life stage with scaled quail chicks exhibiting lower survival rates than bobwhite chicks. It is likely that these differences in chick survival are a result of interspecific differences in habitat selection in combination with differences in home range size and movement. Although, chick survival has been found to be negatively correlated with home range size and daily movement (ring-necked pheasant *Phasianus colchicus*, Hill 1985; greater sage-grouse Gregg 2006), the association between home range size, movement, and the vegetative characteristics of a landscape may be multifaceted and confounding. For example, the vegetative characteristics of a landscape can have significant impacts on resource and invertebrate abundance (Doxon and Carroll 2010, Doxon et al. 2011), which may impact brood home range size and daily movement (DeVos and Mueller 1993), in addition to directly influencing chick

survival rates (Gregg and Crawford 2009). Additionally, survival in gallinaceous chicks has been shown to be correlated to both resource abundance (Gregg and Crawford 2009) and the vegetative characteristics of a landscape (Gregg and Crawford 2009, Pollentier et al. 2014). Differences in the vegetation communities utilized by sympatric species can impact levels of exposure to predation (Ackerman et al. 2014), which may lead to the observed differences in survival estimates at the chick stage.

It is likely that observed differences in survival between northern bobwhite and scaled quail at the chick life stage are not a result of one single factor, but of interspecific variation in habitat selection, daily movements, home range sizes, and resource availability. Scaled quail selected vegetation communities that were more structurally open with less mixed shrub, visual obstruction, and overhead cover than bobwhites. This likely exposed them to higher levels of predation, especially from avian predators. Furthermore, greater daily movements observed in scaled quail potentially exposed chicks to higher levels of predation, especially from avian predators, throughout the day. Mortality, as a result of avian predation, is one of the primary sources of mortalities in quail (Burger et al. 1995), and it was one of the leading causes of mortality within my study. Additionally, the rates of mortality within a species can be influenced greatly by daily movements. For example, greater daily movements have been shown to lead to increased predation rates in adult bobwhites during the breeding season (Lohr et al. 2010). In contrast, with smaller daily movements and greater visual obstruction and mixed-shrub cover providing higher levels of escape cover, bobwhite broods within my study may have been exposed to lower levels of predation risk than scaled quail throughout the initial stages of their lives.

Observed differences in chick survival between closely related sympatric species as a result of differences in habitat selection have been well documented. For example, Ackerman et al. (2014) found that chick survival of sympatric American avocets (*Recurvirostra americana*) and black-necked stilts (*Himantopus mexicanus*) differed significantly, likely as a result of differences in vegetative characteristics within the habitats that the broods occupied. These vegetative differences led to differences in predation risk and exposure (Ackerman et al. 2014). Similarly, Varo (2008) observed significant differences in chick survival between sympatric populations of red-knobbed coots (*Fulica cristata*) and common coots (*Fulica atra*), likely as a result of differences in the resource abundance in the habitats that they occupied. Although, differences in chick survival between sympatric gallinaceous species have not been well studied, or documented, it is likely that they would follow similar trends as waterfowl that also have precocial and highly mobile young. Similar to other studies of sympatric species, differences in survival at the chick life stage were likely a direct result of interspecific variations in resource abundance, vegetation structure, and predator exposure in the vegetation communities utilized.

While differences in survival were observed between the two species at the chick stage, survival was similar at the youth stage. It is possible that scaled quail chicks are exposed to higher levels of predation within their more structurally open habitats, but as chicks age, they may become more vigilant for predators along with having a greater likelihood of evading predators as compared to chicks. This has been observed in snowy plover (*Charadrius nivosus*) chicks as chick survival increased as the chicks developed thermoregulatory independence leading to differences in feeding behavior which lowered predation risk (Colwell et al. 2007). As chicks age, changes in plumage and the differences in feeding behavior can lead to reductions in predation rates (Colwell et al. 2007).

Although it is difficult to directly compare my observed survival rates with previously reported results, my bobwhite youth survival estimates appeared similar to survival estimates from other studies. For example, using flush counts in western Oklahoma, DeMaso et al. (1997) estimated survival probabilities of 0.379 for chicks within the first 20 days of life and 0.968 for chicks between the ages of 21-39 days. Similarly, Suchy and Munkel (2000) estimated survival probabilities of 0.806 for radio-tagged chicks between 21 to 59 days old in Iowa. In western Oklahoma, period survival probabilities were estimated to be 0.627 from 0 to 21 days old and 0.277 from 22 to 120 days old using radio-tagged chicks (Lusk et al. 2005). To my knowledge, estimates of scaled quail chick survival have not been reported, however, one study of scaled quail chick survival found that the percentage of broods with at least one chick at 21 days post-hatch ranged from 10 - 48% (Pleasant et al. 2006). My estimates of chick survival are significantly higher than the previous reported results and these results will provide managers with a better understanding of scaled quail chick survival.

I was unable to investigate survival within the first week following hatching. This was due to high levels of hen abandonment during my study. This was particularly prevalent in scaled quail, as hens were observed abandoning their broods into the care of a secondary brooding adult, such as a putative father, potentially in an effort to re-nest. This behavior would have biased survival estimates low within the first week following hatching. As transmitters are created at increasingly smaller sizes, it will likely be possible to fit transmitters to chicks immediately following hatch. Future research should work to better understand the mechanisms that may impact chick survival in the initial and ecologically critical stages of their lives.

Conclusions

Northern bobwhite and scaled quail appear to be utilizing the landscape in very different ways during the brood-rearing period. The characteristics of a landscape, such as the availability of thermal refugia and high levels of visual obstruction from aerial or terrestrial predation, appear to be more heavily selected by bobwhites than by for scaled quail. The observed levels of habitat partitioning were likely one of the primary factors that led to significant differences in survival in the initial stages of their lives. In order for managers to effectively manage the landscape to benefit both species, they should be aware that activities conducted to benefit one species may be detrimental to a sympatric species.

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Tables and Figures

Table 1. Ground cover categories for vegetation classification of Beaver River Wildlife

Management Area in western Oklahoma.

Land-Cover Class	Vegetation Description
Mixed Shrub/Scrub	Common mixed shrubs include fragrant sumac (*Rhus aromatica*), sand plum (*Prunus angustifolia*), yucca (*Yucca glauca*), western soapberry (*Sapindus drummondii*), Siberian elm (*Ulmus pumila*), and eastern cottonwood (*Populus deltoides*)
Sand Sagebrush	Areas dominated by ground cover of sand sagebrush (*Artemisia filifolia*) cover. Grasses and forbs common but not dominant throughout the WMA
Mixed Grass	Mixed grasses and forbs. Including switch grass (*Panicum virgatum L.*), Indian grass (*Sorghastrum nutans*), big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and giant sandreed (*Calamovilfa gigantean*). Common forbs include sand lily (*Menzelia Spp.*), western ragweed (*Ambrosia psilostachya*), common ragweed (*Ambrosia artemisiifolia*), and sunflower (*Helianthus spp.*)
Shortgrass/Yucca	Areas dominated by common shortgrass species including blue grama (*Bouteloua gracilis*), and buffalo grass (*Bouteloua dactyloides*)
Exposed soil with little vegetation	Areas with high amounts of exposed soil with little vegetative cover
Bare Ground	Exposed soils, roads,parking areas, oil and gas pads
Salt Cedar	Salt cedar (*Tamarix ramosisssima*) dominated grassland
Open Water	Areas of open water, and holding ponds
Housing Developed	Residential areas, houses, and buidings
Agriculture/Food Plot	Areas currently under cultivation in addition to wildlife food plots

Table 2. Period survival estimates (S) for northern bobwhite and scaled quail chicks (20 day) and youths (35 day) by year and pooled across years during the breeding season at Beaver River Wildlife Management Area in western Oklahoma during 2013-2014. Comparisons of period survival estimates with Z-test and corresponding *P*-values (two-tailed) are reported.

Life Stage		**Northern Bobwhite**				**Scaled Quail**			**Z-test**	
		n	**S(t)**	**SE**		**n**	**S(t)**	**SE**	**Z**	**P**
Chick	Pooled	102	0.725	0.068		92	0.488	0.085	3.339	*< 0.001*
	2013	*45*	*0.622*	*0.077*		*70*	*0.500*	*0.145*	0.949	*0.343*
	2014	*57*	*0.813*	*0.103*		*22*	*0.481*	*0.098*	3.984	*< 0.001*
Youth	Pooled	94	0.788	0.086		57	0.795	0.110	-0.090	*0.928*
	2013	*45*	*0.742*	*0.118*		*11*	*0.818*	*0.116*	-0.539	*0.590*
	2014	*49*	*0.824*	*0.105*		*46*	*0.789*	*0.113*	0.377	*0.706*

Table 3. Estimated mean (+/- SE) home range size (ha) and composition of the predominant vegetation types within home ranges of northern bobwhite (NOBO) and scaled quail (SCQU) broods during chick (0-30 days old) and youth (31-80 days old) life stages at Beaver River Wildlife Management Area in western Oklahoma from 2012 to 2014. Results of two-sample t-tests (P-values, two-tailed) and degrees of freedom (df) between species at each life stage are reported.

Life Stage[a]	Home Range (ha)	% Mixed Shrub	% Sand Sagebrush	% Mixed Grass	% Shortgrass/Yucca	% Exposed Soil/Little Veg.
NOBO Chick	20.62 ± 2.36	13.69 ± 3.59	37.79 ± 2.55	26.72 ± 2.34	17.64 ± 1.66	1.22 ± 0.16
SCQU Chick	32.09 ± 5.45	1.29 ± 0.48	25.59 ± 4.36	29.71 ± 2.66	36.02 ± 5.22	2.66 ± 0.87
df	27	29	33	48	24	21
t	-1.931	3.429	2.413	-0.838	-3.355	-1.627
P[b]	0.064	0.002	0.022	0.406	0.003	0.119
NOBO Youth	15.36 ± 3.04	9.97 ± 3.43	38.59 ± 3.22	27.99 ± 2.52	18.28 ± 2.63	1.68 ± 0.26
SCQU Youth	66.34 ± 14.54	1.52 ± 0.73	22.42 ± 5.17	26.75 ± 2.84	42.54 ± 7.24	3.04 ± 0.84
df	12	19	28	28	14	13
t	-3.432	2.407	2.806	0.322	-3.150	-1.545
P[b]	0.005	0.026	0.009	0.750	0.007	0.146

[a]Sample sizes for NOBO chick = 29, SCQU chick = 21, NOBO youth = 18, and SCQU youth = 12.

[b]P-value for 2-tailed t-test.

Table 4. Mean (± SE) percentages of ground cover (shrubs, grass, forb, legume, bare ground and leaf litter) and angle of obstruction (°) values at northern bobwhite and scaled quail brood sites from 2012 to 2014 at Beaver River WMA in western Oklahoma. Results of two-sample t-tests (P-values, two-tailed), and degrees of freedom (df) between active ([sunrise – 11:00, and 16:01-sunset]), and loafing (11:01-16:00) locations are reported.

Time Period[a]	Shrub Cover	Grass	Forb	Legume	Bare Ground	Leaf Litter	Angle of Obstruction
NOBO Active	25.13 ± 2.39	15.29 ± 1.44	19.95 ± 1.45	0.05 ± 0.03	26.34 ± 1.73	54.74 ± 2.26	44.24 ± 1.69
NOBO Loafing	38.12 ± 4.13	13.04 ± 2.15	12.37 ± 1.71	0.01 ± 0.01	26.4 ± 2.33	57.11 ± 3.65	50.57 ± 2.32
df	134	134	134	105	134	134	134
t	-2.891	0.875	3.117	1.101	-0.017	-0.571	-2.152
P[b]	*0.004*	*0.383*	*0.002*	*0.273*	*0.986*	*0.569*	*0.033*
SCQU Active	14.12 ± 1.64	13.43 ± 1.41	16.38 ± 1.32	0.24 ± 0.22	36.45 ± 1.65	41.32 ± 2.06	34.45 ± 1.33
SCQU Loafing	15.19 ± 2.37	15.35 ± 1.91	17.42 ± 1.81	0.10 ± 0.07	35.4 ± 2.14	39.85 ± 2.64	37.38 ± 2.06
df	155	155	155	115	155	155	110
t	-0.384	-0.822	-0.473	0.578	0.391	0.439	-1.195
P[b]	*0.701*	*0.412*	*0.637*	*0.564*	*0.696*	*0.661*	*0.235*

[a]Sample sizes for NOBO Active = 93, NOBO Loafing = 43, SCQU Active = 95, and SCQU Loafing = 62.

[b]P-value for 2-tailed t-test.

Table 5. Visual obstruction profiles (± SE) of northern bobwhite (NOBO) and scaled quail (SCQU) active (sunrise – 11:00, and 16:01-sunset) and loafing (11:01-16:00) brood locations between June-August 2012-2014 at Beaver River WMA in western Oklahoma. Strata include; 1 = 0-10 cm aboveground, 2 = >10-20 cm aboveground, 3 = >20-30 cm aboveground, …., 12 = >110-120 cm aboveground. Results of two-sample t-tests (P-values, two-tailed), and degrees of freedom (df) between time periods are reported.

Stratum[a]	1	2	3	4	5	6	7	8	9	10	11	12
NOBO Active	95.00 ± 0.66	90.67 ± 1.09	79.17 ± 2.11	70.97 ± 2.55	61.02 ± 2.82	51.74 ± 2.93	41.50 ± 3.05	33.67 ± 3.04	27.99 ± 3.06	25.31 ± 3.11	21.18 ± 2.96	19.53 ± 3.01
NOBO Loafing	94.60 ± 1.09	91.27 ± 1.58	85.35 ± 2.70	78.81 ± 3.38	70.77 ± 3.84	62.24 ± 3.91	52.33 ± 4.41	45.93 ± 4.76	41.77 ± 4.96	37.66 ± 5.06	34.56 ± 5.09	32.44 ± 5.08
df	134	134	134	134	134	134	134	134	134	134	134	134
t	0.324	-0.309	-1.713	-1.783	-1.988	-2.073	-2.006	-2.222	-2.450	-2.160	-2.404	-2.303
P[b]	0.747	0.758	0.089	0.077	0.049	0.040	0.047	0.028	0.016	0.033	0.018	0.023
SCQU Active	88.65 ± 1.87	78.54 ± 2.46	63.09 ± 3.17	53.16 ± 3.34	38.85 ± 3.11	29.37 ± 2.86	20.20 ± 2.41	15.02 ± 2.26	9.79 ± 1.97	6.78 ± 1.66	5.22 ± 1.50	4.49 ± 1.39
SCQU Loafing	85.02 ± 2.95	76.66 ± 3.69	65.16 ± 4.00	58.67 ± 4.10	48.73 ± 3.79	39.15 ± 3.44	27.60 ± 3.40	21.28 ± 3.13	16.77 ± 2.90	13.78 ± 2.64	11.81 ± 2.56	9.92 ± 2.38
df	108	113	155	155	155	155	155	155	155	108	102	102
t	1.037	0.423	-0.408	-1.040	-2.009	-2.172	-1.823	-1.663	-2.062	-2.244	-2.216	-1.969
P[b]	0.302	0.673	0.684	0.300	0.046	0.031	0.070	0.098	0.041	0.027	0.029	0.052

[a]Sample sizes for NOBO Active = 93, NOBO Loafing = 43, SCQU Active = 95, and SCQU Loafing = 62.

[b]P-value for 2-tailed t-test.

APPENDICES

Appendix A

TEMPORARY COMMUNAL BROODING IN NORTHERN BOBWHITE AND
SCALED QUAIL BROODS AS A RESPONSE TO ATYPICALLY COOL
TEMPERATURES

Abstract

Communal brooding is a common alternative brooding strategy observed in bird species
with precocial young. Across many species, communal broods, can be as temporary as a
15 minute bout in response to a predation event or as permanent as several months until
chicks reach adulthood. While the occurrence of long-term communal brooding has been
documented in numerous waterfowl species and to a lesser extent gallinaceous species,
the occurrence and mechanisms leading to temporary or short-term communal broods is
less understood. During the 2013 and 2014 breeding seasons, I observed temporary
communal brooding in two Northern Bobwhite (*Colinus virginianus*) broods and one
Scaled Quail (*Callipepla squamata*) brood. I postulate that these occurrences of
temporary communal brooding were a direct result of cool weather conditions observed
at intermittent intervals throughout the breeding season.

Introduction

Brood amalgamation is a common brood rearing strategy that has been documented in numerous gallinaceous and waterfowl species (Mills and Rumble 1991, Lott and Mastrup 1999, Brooks and Rollins 2007, Wong et al. 2009, Dahlgren et al. 2010). These amalgamations can be classified into four forms including kidnapping, adoption, creching, and gang-brooding (Eadie et al. 1988, Afton and Paulus 1993, Faircloth 2005). Amalgamations of particular interest in this study are gang brooding and creching. I define temporary communal brooding as the occurrence of short-term gang brooding or creching that is non-permanent and is followed by brood separation. Gang brooding occurs when two or more adults combine their respective broods into one group, and creching occurs when two or more unrelated offspring are cared for by two or more adults which they may or may not be related to (Eadie et al. 1988, Afton and Paulus 1993, Faircloth et al. 2005). Communal brooding has been documented in numerous quail species, including northern bobwhite (*Colinus virginianus*), California Quail (*Callipepla callifornica*), and Gambels Quail (*C. gambelii*) (Brown et al. 1998, Lott and Mastrup 1999, Faircloth et al. 2005, Brooks and Rollins 2007, Calkins 2007), however the mechanisms that facilitate these amalgamations are still unclear.

Communal broods can be as temporary as a few minutes or as long as an entire brooding period (Boos et al. 1989, Brooks and Rollins 2007), and there are a number of theories that have been presented to explain the short and long-term occurrences of this breeding strategy. In California quail, brooding adults engaged in communal brooding in an effort to increase their survival by reducing time spent being vigilant, thereby

providing the adults additional time for feeding and individual care (Lott and Mastrup 1999). In Northern Bobwhites, it is believed that gang brooding increases reproductive flexibility (Brooks and Rollins 2007) and northern bobwhite hens have been documented abandoning chicks in an effort to re-nest (Curtis et al. 1993, Suchy and Munkel 1993, Burger et al. 1995). In Mallards (*Anas platyrhnchos*) temporary communal broods lasted as little as 15 minutes, serving as a mechanism for predator protection (Boos et al. 1989). In King Eider (*Somateria spectabilis*) temporary communal brooding allowed hens to forage independently or to search out a better brooding territory while leaving in the care of other females for 3-4 days (Mehl et al. 2007). Finally, adult Bristle-thighed Curlews (*Numenius tahitiensis*) have been hypothesized to engage in temporary communal brooding in order to increases vigilance from predation (Lanctot et al. 1995).

While temporary communal broods have been documented in numerous waterfowl species, little information exists in regards to the occurrence and the mechanisms that may facilitate short-term communal brooding in gallinaceous bird species. Here, I document occurrences of temporary communal brooding in northern bobwhite and scaled quail in western Oklahoma, and postulate a mechanism that may facilitate this strategy.

Materials and Methods

As part of a companion research project investigating chick survival and reproductive behavior, adult northern bobwhite and scaled quail were captured at Beaver River Wildlife Management Area in western Oklahoma during the 2013 and 2014 breeding season. Adults were fitted with 7 g necklace style collars (Advanced Telemetry

Solutions, Isanti, MN) and nests were located via telemetry and following location, checked daily. Following hatching, I radio-tracked adults with broods daily. Once chicks reached an age of 8 - 12 days old, I captured the chicks, during a nightly capture event, and fitted a 0.45 g suture-style transmitter to them. The transmitters had an expected battery life of 21 - 23 days (American Wildlife Enterprises, Monticello, FL). Weather data was collected using a WeatherHawk 232 (WeatherHawk, Logan, Utah) weather station that was located on the study site.

Observations

During the study, I conducted 46 (26 bobwhite, 20 scaled quail) successful brood captures. During these captures events, I observed temporary communal brooding on three occasions. The first occurrence of temporary communal brooding occurred on 9 June 2014. Two radio-marked female scaled quail had been brooding their chicks in close proximity (within 100 m) of each other during daytime radio-tracking events, but during the capture event both broods were observed roosting together. During the capture event, I was able to capture five chicks, but it was probable that more chicks were present. Following transmitter attachment, the broods remained brooding together until 11 June. When the broods separated, one adult had one radio-marked chick, while the second adult had four of the radio-marked chicks and the brood did not rejoin thereafter. Nightly temperatures ranged from 11.3 to 12.7 °C, which were approximately 4-5 °C lower than the minimum average nightly temperature observed throughout June 2014.

A second occurrence of temporary communal brooding occurred on 17 July 2014. One radio-marked adult bobwhite male with 6 chicks was located roosting with an

unmarked female brooding nine chicks. Previous locations did not indicate that this brooding adult was with the adult male, as chicks captured with the hen were likely only 3-4 days old based upon their mass at capture (7.7-8.6 g). The two broods separated the following day and the unmarked female and her brood were not observed with the brood on the following night when they were checked unobtrusively with a FLIR Thermal Imaging Camera i7® (FLIR Systems, Wilsonville, Oregon). Temperatures during the night of capture were at a 3-week low of 13.9 °C, approximately 4 °C lower than the minimum average nightly temperature observed in July 2014.

A third occurrence of communal brooding occurred on 28 September 2013. During the capture event, the female brooding adult bobwhite, with five chicks, was located roosting with two additional adult males. These additional adults had not been observed with the brood during prior daily tracking events. Minimum temperatures during the night of capture were 9.4 °C, which was the coldest temperature during all capture events. While this occurrence may not specifically fall under the conventional designation of gang brooding or creching, this is still a form of cooperative brooding as these additional adults are providing care in the form of thermal protection, albeit temporarily, to the chicks. The additional two adults were not observed with the brood again during a subsequent daytime brood flush, however loose covey formation was observed throughout the study area during this time period and it is possible that the additional brooding males rejoined the brood on following days.

Discussion

The occurrence of temporary communal brooding observed within our study was likely a result of atypically cold temperatures observed occasionally throughout the breeding season. As with most precocial species, northern bobwhite and scaled quail chicks typically leave the nest hours after hatching, and immediately become exposed to predation risks and weather events. As a result, these chicks are dependent upon the brooding adult throughout the day, but especially during thermal extremes, as chicks are unable to completely thermoregulate until reaching an age of 30 days old (Borchelt and Ringer 1973). A quail chick's small mass and juvenile plumage increases their vulnerability to atypical fluctuations in temperature (Spiers et al. 1985). In particular, cool temperatures can lead to reductions in growth rates of quail chicks (Krijgsveld et al. 2003) in addition to negatively impacting chick survival. While studying Ring-necked Pheasants (*Phasianus colchicus*), Riley et al. (1998) found that exposure to cold and precipitation negatively impacted chick survival. Similarly, in Wild Turkeys (*Meleagris gallopavo*) cold weather and precipitation increased poult mortality, especially in chicks greater than 12 days old, when chick size prevents efficient brooding by the hen (Healy and Nenno 1985, Healy 1992). In addition to the effect of temperature on chicks, cool temperatures can also negatively impact brooding adults. Brooding can be energetically costly to the adults, especially during periods of cool temperature and acute thermal stress (Pearson 1994). Brooding King Quail (*Coturnix chinensis*) hens have been shown to have significantly higher energetic demands than non-brooding adults during periods of

low temperatures (Pearson 1994). It may be important for brooding adult quail to utilize alternative brooding strategies, including temporary communal brooding.

The three occurrences of communal brooding in our study were observed on atypically cold nights with temperatures 4-5 °C lower than average minimum nightly temperatures, and these cool temperatures likely facilitated the temporary communal brooding observed. While adults during the non-breeding season gain thermoregulatory benefits from communal roosting in coveys, this roosting strategy can only be achieved during the breeding stage through bi-parental care or communal brood rearing. One of the principal benefits of communal roosting in birds is a reduction in thermoregulation demands (Beauchamp 1999), and due to their small size, cold temperatures are one of the leading causes of mortality in bobwhites during the non-breeding season (Robel and Kemp 1997). While bi-parental care was commonly observed in both bobwhite and scaled quail, the three broods in which I observed communal brooding had been brooding independently, without the assistance of a secondary brooding adult until the date of capture. It is likely that broods with only one brooding adult, are more vulnerable to atypically cool temperatures than are broods with two brooding adults. Through temporary communal brooding on cool nights, adults can reduce energetic demands, and increase chick survival.

When chicks are young and temperatures become atypically cold, brooding adults appear to form temporary communal broods in an effort to increase chick survival and reduce energetic demands. Chicks and brooding adults roosting within these temporary communal broods likely gain the added advantage of increased thermal protection, and

reduced energetic demands on cool nights. Future research should work to investigate

the effect that temporary communal brooding can have on chick and adult survival during

the breeding season.

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