NORTHERN BOBWHITE OFFSPRING SURVIVAL RELATED TO GROWTH AND PARENTAL INVESTMENT FOLLOWING TRANSLOCATION

by

KYLE DURAN LUNSFORD

(Under the Direction of James Alan Martin)

ABSTRACT

The continued decline of northern bobwhite populations has energized the use of reintroduction strategies coupled with habitat management to achieve restoration goals. We sought to determine if restocking of wild northern bobwhites via translocation impacted survival and growth rates of translocated northern bobwhite chicks or altered parental investment strategies (brood defense behaviors) compared to resident counterparts. There were no differences in chick survival rates of translocated or resident bobwhites over our two-year study; however, survival estimates were lower in 2017. We found that increasing age and tarsus length positively impacted daily survival rates of bobwhite chicks. Offspring growth rates of translocated bobwhites were lower than resident cohorts; however, these reduced growth rates did not carry any survival consequences. Additionally, we found no difference in brood defense behaviors of translocated bobwhites. These results indicate that translocation does not alter behavioral patterns or negatively impact offspring survival rates in wild bobwhites.

INDEX WORDS: translocation, reintroduction, northern bobwhite, offspring, restoration, parental investment

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DEDICATION

I'd like to dedicate this thesis to my great grandmother Ida Lunsford, and my other ancestors who spent many hours working in tobacco fields to make a better life for their children. The sacrifices they made for their children continue to drive me to succeed, and remind me that no obstacle in life is insurmountable.

Security ... what does this word mean in relation to life as we know it today? For the most part, it means safety and freedom from worry. It is said to be the end that all men strive for; but is security a utopian goal or is it another word for rut?

Let us visualize the secure man; and by this term, I mean a man who has settled for financial and personal security for his goal in life. In general, he is a man who has pushed ambition and initiative aside and settled down, so to speak, in a boring, but safe and comfortable rut for the rest of his life. His future is but an extension of his present, and he accepts it as such with a complacent shrug of his shoulders. His ideas and ideals are those of society in general and he is accepted as a respectable, but average and prosaic man. But is he a man? has he any self-respect or pride in himself? How could he, when he has risked nothing and gained nothing? What does he think when he sees his youthful dreams of adventure, accomplishment, travel and romance buried under the cloak of conformity? How does he feel when he realizes that he has barely tasted the meal of life; when he sees the prison he has made for himself in pursuit of the almighty dollar? If he thinks this is all well and good, fine, but think of the tragedy of a man who has sacrificed his freedom on the altar of security, and wishes he could turn back the hands of time. A man is to be pitied who lacked the courage to accept the challenge of freedom and depart from the cushion of security and see life as it is instead of living it second-hand. Life has by-passed this man and he has watched from a secure place, afraid to seek anything better What has he done except to sit and wait for the tomorrow which never comes?

Turn back the pages of history and see the men who have shaped the destiny of the world. Security was never theirs, but they lived rather than existed. Where would the world be if all men had sought security and not taken risks or gambled with their lives on the chance that, if they won, life would be different and richer? It is from the bystanders (who are in the vast majority) that we receive the propaganda that life is not worth living, that life is drudgery, that the ambitions of youth must he laid aside for a life which is but a painful wait for death. These are the ones who squeeze what excitement they can from life out of the imaginations and experiences of others through books and movies. These are the insignificant and forgotten men who preach conformity because it is all they know. These are the men who dream at night of what could have been, but who wake at dawn to take their places at the now-familiar rut and to merely exist through another day. For them, the romance of life is long dead and they are forced to go through the years on a treadmill, cursing their existence, yet afraid to die because of the unknown which faces them after death. They lacked the only true courage: the kind which enables men to face the unknown regardless of the consequences.

As an afterthought, it seems hardly proper to write of life without once mentioning happiness; so we shall let the reader answer this question for himself: who is the happier man, he who has braved the storm of life and lived or he who has stayed securely on shore and merely existed?

-- "Security" by Hunter S. Thompson (1955)

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challenging me to discover what I enjoy and what mark I want to leave on this field. I look forward to working with you both in the future.

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I express great gratitude to all my family and friends who supported me in my pursuit of this degree: Percy, Vivien, Hannah, Maw-Maw, Paw-Paw, Grandma James, Craig, Steve, Cindy, Leah, David/Karen/Jason/Patrick Wells, Matt Armstrong, Dustin Dowless, Aaron/Cassie Griffith, and many others. I'd like to especially thank my parents, Percy and Vivien, for teaching me discipline and keeping me grounded throughout my career and taught me that the only way to succeed in life is through dedication and hard work. Your advice and guidance throughout all of life's twists and turns have been invaluable in shaping who I am today. Most importantly, I'd like to thank God for providing me the opportunity to pursue my dreams and bring many others to enjoy the passion for the world He created.

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CHAPTER 1

Introduction

Reintroductions of wildlife species have been occurring for over 100 years with mixed results (Armstrong and Seddon 2008). Reintroduction failures may owe to the lack of thorough experimental design and post-release population monitoring to determine factors limiting reintroduction success (Lipsey et al. 2007, Seddon et al. 2007). Population monitoring post-translocation is imperative to determining if vital rates of reintroduced individuals can establish and maintain viable populations (World Pheasant Association and International Union for the Conservation of Nature/Species Survival Commission Re-introduction Specialist Group 2009). Reintroduction success is contingent upon three important criteria: survival of reintroduced individuals, evidence of successful breeding in reintroduced populations, and long-term population persistence (World Pheasant Association and International Union for the Conservation of Nature/Species Survival Commission Re-introduction Specialist Group 2009). We hope to estimate offspring survival rates to: determine if translocated northern bobwhites (*Colinus virginianus*) can successfully raise offspring post-release, produce offspring as well as resident counterparts, and assist in determining short-term population dynamics after release. These estimates will be imperative to determining project success after three years of wild bobwhite translocation to our study site.

Bobwhite Translocation History

In 1950, bobwhites were translocated across the state of Wisconsin to augment winter mortality and recover extirpated populations (Kabat and Thompson 1963, Martin et al. 2017). Translocations were also attempted in West Virginia and Indiana to augment populations after over-winter declines (Martin et al. 2017). The Ohio Department of Natural Resources (ODNR) also attempted bobwhite translocation following failures of released captive-reared populations but translocated populations did not achieve long-term persistence (Wiley et al. 2017). These studies cited short-term abundance increases followed by declines due to degraded or suboptimal habitat, dispersal, and stochastic events as reasons for lack of long-term population persistence (Kabat and Thompson 1963, Martin et al. 2017, Wiley et al. 2017). Additionally, post-translocation monitoring was identified as an important tool needed to determine if bobwhites observed in subsequent years were progeny of translocated individuals.

In later studies, restocking (augmentation of populations through translocation) efforts allowed comparison of vital rates between resident and translocated individuals. A study in Rio Grande Plains ecoregion of Texas found that survival rates (release to 12 weeks) of translocated bobwhites were not different from residents (Perez et al. 2002). Translocation of bobwhites also occurred in the post oak-savannah ecoregion of Texas where translocated bobwhites had lower survival and reproductive rates, and lower overall abundance than resident bobwhites (Scott et al. 2013). Scott et al. (2013) noted that habitat fragmentation at the release site may explain lower vital rates of translocated bobwhites, indicating the habitat conditions at release sites remains an important consideration when planning translocations. There have also been some success stories regarding translocation of wild bobwhites. In Tennessee, Jones (1999) found that survival, home range sizes, and reproductive metrics were similar between translocated and resident bobwhites. Other studies have documented that translocated bobwhites have similar demographic rates as resident individuals, and can contribute to short-term population growth in fragmented and intensively managed landscapes (Terhune et al. 2006a, 2010). These success stories offer some promise that translocation may be able to restore bobwhite populations where habitat management for bobwhites has been implemented and populations exist.

Knowledge Gaps

The advent of reintroduction biology (Seddon et al. 2007) has highlighted the need for scientific rigor in population restoration techniques, and currently bobwhite literature only has a handful of studies implementing good experimental design for testing hypotheses pertinent to reintroduction success. Adult survival and space use have been the focus of much of the bobwhite translocation literature thus far, with some comparisons of reproductive metrics between resident and translocated cohorts (Kabat and Thompson 1963, Terhune et al. 2006b, a, 2010, Scott et al. 2013, Wiley et al. 2017). Offspring survival is an important demographic in determining short and long-term trends in bobwhite populations (Roseberry 1974, Roseberry and Klimstra 1984). Overall, direct survival estimates and observations of brood dynamics in northern bobwhites are limited in the scientific literature (Suchy and Munkel 2000, Lusk et al. 2001) emphasizing the need to further understand this complex life stage. Furthermore, survival rates of northern bobwhite chicks have not been estimated post-translocation. This is an important knowledge gap in not only bobwhite ecology but reintroduction biology as well.

The focus of my thesis is to first estimate and compare chick survival rates of translocated and resident bobwhites. We sought to determine important intrinsic and extrinsic factors that may impact survival rates among resident and translocated progeny. Intrinsic factors such as chick growth rates and body size may provide a measure of how translocated bobwhites are adapting to a novel landscape by their ability to locate important food and cover resources conducive to offspring survival. Additionally, we identified important behavioral patterns (offspring defense behaviors) in resident and translocated bobwhites to determine if translocation impacts parental investment strategies. Our study site has been under longleaf pine-savanna restoration since 2011 and close examination of aerial imagery suggested heterogeneity in vegetation recovery patterns even with intensive habitat management. These differences may be due to variation in soil productivity (extremely sandy soils), or landscape legacies due to past management (herbicide use, pine straw raking, etc.) or lack thereof. We used vegetation structure measures derived from satellite imagery to evaluate how vegetation structure post-restoration impacts chick survival. This information will help broaden the published literature on northern bobwhite population dynamics post-translocation and give managers some insight as to how bobwhites are able to adapt and breed in novel landscapes following habitat restoration.

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CHAPTER 2

Offspring Survival Rates Post-Translocation: Influence of Intrinsic and Extrinsic Factors

Population restoration techniques—such as reintroduction and restocking—can help populations reach desired levels after habitat management. Translocation is the movement of individuals from source sites to donor sites with the intention of reintroducing (restoring extirpated populations) or restocking (releasing into an existing population to avoid problems associated with low populations) populations in critical need for restoration (International Union for the Conservation of Nature 1987, Seddon 2010, Martin et al. 2017). The IUCN *Guidelines for the Reintroduction of Galliformes for Conservation Purposes* specified 3 stages in establishing reintroduction success, "survival of founders, evidence of breeding by founders, and long-term persistence of translocated population" (World Pheasant Association and International Union for the Conservation of Nature/Species Survival Commission Re-introduction Specialist Group 2009). Estimation of population vital rates is imperative to evaluating the short- and long-term success of reintroduction efforts (World Pheasant Association and International Union for the Conservation of Nature/Species Survival Commission Re-introduction Specialist Group 2009).

Translocation has been used to reintroduce or restock northern bobwhite (*Colinus virginianus*) populations with mixed results (Kabat and Thompson 1963, Jones 1999, Perez et al. 2002, Terhune et al. 2006*a*, *b*, 2010, Scott et al. 2013). These studies compared vital rates of translocated to resident bobwhites, focusing on survival and reproductive effort/success of translocated individuals; however, survival of offspring for translocated individuals has not been studied (Jones 1999, Perez et al. 2002, Terhune et al. 2006*a*, *b*, 2010, Scott et al. 2013).

Offspring survival influences parental fitness, and is an important driver of population growth rates (Wisdom and Mills 1997, Sandercock et al. 2005). Furthermore, brood ecology is a glaring knowledge gap in the life history of northern bobwhites (Roseberry and Klimstra 1984, DeVos and Mueller 1993, DeMaso et al. 1997, Brennan 1999, Smith et al. 2003) and the development of capture techniques (Smith et al. 2003) and micro-transmitters has allowed us gain valuable information (survival, movement, growth rates, etc.) about this critical life stage (Suchy and Munkel 2000, Lusk et al. 2005). These data will allow for comparisons between resident and translocated offspring to help determine if translocated bobwhites are able to raise offspring successfully and contribute to population growth.

Avian growth rates may vary among populations and species, and could be driven by a variety of selective pressures (Gebhardt-Henrich and Richner 1998). Observed growth rate variations may influence individual fitness, and ultimately population growth (Gebhardt-Henrich and Richner 1998). Variations in offspring growth rates exist in species with precocial young (Owen and Black 1989, Francis et al. 1992, Schmutz 1993, Kamps et al. 2017), and may be expressed by variety of morphometries (mass, tarsus, wing-chord, etc.). These variations may drive differences in offspring survival pre-fledging and post-fledging (Ross and Mclaren 1981, Owen and Black 1989, Francis et al. 1992, Schmutz 1993, Morrison et al. 2009). Reduced growth rates may increase time-to-fledging in bobwhite chicks (Gebhardt-Henrich and Richner 1998), which could increase the amount of parental investment needed to raise offspring to independence. Stressors from translocation and lack of site familiarity may exacerbate differences in offspring survival and growth rates of translocated bobwhites. Increased investment in slow-growing offspring (longer time-to-fledging) may limit renesting opportunities in translocated bobwhites despite having long breeding seasons (Roseberry and Klimstra 1984).

Limited renesting opportunities may impact the ability of translocated bobwhite to contribute to population growth and recovery. However, intrinsic factors may not be the only explanation to variations in offspring survival and growth rates, extrinsic factors such as weather may drive these variations.

Precipitation is thought to increase mortality rates of bobwhite chicks due to the wetting of natal down feathers, and potential drowning (Stoddard 1931, Lusk et al. 2001, Hernández et al. 2002). Hypothermia (direct effect) and increased susceptibility to disease and predation (indirect effects) are associated with exposure especially before chicks can fully thermoregulate (Stoddard 1931, Paasivaara and Pöysä 2007). Bobwhite chicks do not achieve full thermoregulatory ability until reaching an age of 35-42 days (Spiers et al. 1985), and require brooding by the adult to maintain optimal body temperature. Adverse weather conditions (rain and colder temperatures) increase the amount of brooding time needed to maintain body temperatures thus reducing foraging opportunities during this critical life stage (Theberge et al. 1973, Pedersen and Steen 1979, Erikstad and Spidsø 1982, Erikstad and Andersen 1983, Ludwig et al. 2010). Growth and survival rates could be impacted if adverse weather conditions limit foraging opportunities during when a protein-rich diet is needed for rapid physiological development (Stoddard 1931, Nestler et al. 1942, Hurst 1972). Limited foraging opportunities and thermoregulatory demands of bobwhite chicks emphasize the importance of quick location of food and cover resources when confronted with adverse weather conditions. Lack of site familiarity among translocated bobwhites may exacerbate the effects of rainfall events if brooding adults are not able to find food and cover resources efficiently. Providing quality habitat is imperative to translocation success by providing adequate resources to maximize survival and reproduction (Terhune et al. 2006*b*), especially in species like bobwhite where offspring survival rates are low (Yates et al. 1995).

Vegetation structure is an important component of habitat quality for many species (Nudds 1977, Cody 1981). Properties that undergo habitat restoration for bobwhites are concerned with establishing herbaceous vegetation that provides the cover and food resources necessary for survival and reproduction. The Normalized Difference Vegetation Index (NDVI) has been used in recent ecological studies as an index that links temporal aspects of vegetation development (greenness) to population demographics and individual growth (Pettorelli et al. 2005, 2007). Site characteristics (low productivity soils, etc.) may impede growth of early herbaceous vegetation leading to increased fragmentation (bare ground) across the landscape. Texture measures may provide accurate measures of horizontal vegetation structure when small sampling window sizes are used in conjunction with high resolution imagery (Wood et al. 2012), which may help identify bare ground distribution within chick home ranges. Configuration and composition of habitat in our study site may affect the ability of translocated bobwhites to locate resources efficiently (Schmitz and Clark 1999, Poysa and Paasivaara 2006).

The overall goal of this study was to compare offspring growth and survival rates of translocated and resident bobwhites following translocation. We tested the site familiarity hypothesis (Yoder et al. 2004, Marable et al. 2012) to determine if translocated bobwhites are able to raise offspring similar to resident bobwhites. Comparison of offspring survival rates and physiological development provide reflections of how well translocated bobwhites are able to locate important food and cover resources compared to resident cohorts. In addition, site familiarity may drive differences in selection of landscape characteristics within brood home ranges that may have implications for offspring survival. Perceptual errors may drive translocated bobwhites to use lower quality habitat due to disparities in donor and release site characteristics. Estimation of offspring survival rates will help evaluate if translocated bobwhites are successfully reproducing, and if their survival rates are comparable to our resident population (World Pheasant Association and International Union for the Conservation of Nature/Species Survival Commission Re-introduction Specialist Group 2009). In addition, offspring survival rates will provide an important vital rate for modeling translocated populations post-release.

STUDY AREA

Our study was conducted on a private plantation located in Brunswick County, North Carolina USA, located in the Carolina flatwoods ecoregion (Griffith et al. 2002). Average temperature ranges for Brunswick County, NC range from 18°–34°C in June–September (National Climate Data Center, National Oceanic and Atmospheric Administration). In 2016, our study site averaged 0.63 cm of rainfall per day (0–20.42 cm) and 0.50 cm/day (0–5.54 cm/day) in 2017 (National Climate Data Center, National Oceanic and Atmospheric Administration). The study area encompasses 2586 ha and consists of pine flatwoods and savannas as well as interspersed hardwood drains, Carolina bays and pocosin wetlands (Griffith et al. 2002). Pine savannas and flatwoods consist mainly of longleaf pine (*Pinus palustris*), lobolly (*Pinus taeda*), and live oaks (*Quercus virginiana*) that were thinned to a low basal area (BA = 1.2-2.4 m^2 ha^{-1}) to promote an understory of herbaceous vegetation. Primary understory species in upland areas are wiregrass (*Aristida stricta*), little bluestem (*Schizachyrium scoparium*), as well as variety of shrubs including huckleberry (*Gaylussacia* spp.), wax myrtle (*Myrica cerifera*), and gallberry (*Ilex glabra*). Prior to 2011, the property was mainly used for timber and pinestraw production. In 2011, restoration of the longleaf pine-savanna began and included extensive planting of native warm-season grasses, timber thinning, prescribed fire (2-year rotation), mowing, hardwood control, supplemental feeding, fallow field implementation, and meso-mammal trapping (Jackson et al. 2018). Source sites were located in the Red Hills region of northern Florida within the southeastern Coastal Plain, and have historically practiced intensive management for bobwhites. Habitat management of source sites include maintenance of low basal area upland pine forests (e.g. 3–9 m^2 ha^{-1}) dominated by shortleaf (*Pinus echinata*) and loblolly (*Pinus taeda*) pines. Early successional vegetation communities such as bunchgrasses (*Andropogon sp.)*, forbs (*Solidago* spp., *Chamaecrista fasciculata*, *Ambrosia artemisifolia*), and blackberry (*Rubus* spp.) are maintained through a 2-year prescribed fire return interval and mechanical control (mowing, roller-chopping, herbicide, etc.). Hardwood hammocks and drains are also interspersed throughout the landscape. Additionally, properties maintain a patchwork of annually-disked fallow fields throughout upland pine communities (Staller et al. 2005, Ellis-Felege et al. 2012, Jackson et al. 2018). Our study site was divided into 4 release areas: Control, RA1, RA3, and RA4 (Figure 1). Release areas were sections of the study site that received translocated bobwhites over the 2-year study. Release areas were selected for translocation based on year: RA3 – 2016, RA4 – 2017, and RA1 – 2016/2017. The Reference Area was allowed to naturally recolonize starting in 2014, and received no translocations over the course of study; however, 300 wild bobwhites and 2000 F1 bobwhites (Cass 2008, Palmer et al. 2012) were translocated there in 2014.

METHODS

Capture

We captured resident bobwhites during March (spring trapping period) and December (winter trapping period), 2016 and 2017, using the "walk-in" style funnel traps baited with wheat or corn (Stoddard 1931). Traps were covered using pine limbs to conceal traps from mammalian and avian predators, and decrease stress on captured bobwhites (Terhune et al. 2007). We aged (adult/juvenile) individuals by examining primary coverts (Petrides and Nestler 1943) and determined sex by examining throat patch and superciliary coloration. After data collection, we attached 6-g (< 5% body weight) necklace-style radio transmitters (Holohil Systems, Carp, Ontario, Canada) to a subset of captured bobwhites (≥ 132g). The trapping procedure was the same for the donor and source sites. Our trapping, handling, and tagging procedures were approved by the Florida Wildlife Commission (Northern Bobwhite Trapping Permit #: SPGS-14-43) and the University of Georgia Institutional Animal Care and Use Committee (A2015 08-008-Y3-A0). Translocation permits were approved by the Florida Wildlife Commission (Translocation Permit #: QT-16-01) and North Carolina Wildlife Resources Commission (Permit #: 17-CSP00501).

Bobwhites were translocated (2016: n = 266, 2017: n = 270) annually over the 2-year study from 3 properties in the Red Hills region of northern Florida. Two properties were located in Leon County, FL, and the third property was located in Jefferson County, FL approximately 32 km away. Bobwhites were transported using methodology described in Terhune et al. (2010). Capture and translocation of wild bobwhites occurred in March of 2016 and 2017. Release sites for translocated bobwhites were located near the centroid of the release area to reduce the chance of individuals leaving the study site.

Telemetry

We located adults at least 2-3 times per week during the breeding season (1 April - 1 October) using the homing method (White and Garrott 1990, Kenward 2001). Hand-held 3-element Yagi antennas and Lotek Telemetry Receivers (Lotek Wireless, St. Johns, New Foundland, Canada) were used to locate birds over the duration of the study. Homing distances were around 25-m to minimize any location bias and ensure habitat classifications were correct. When radio-tagged bobwhites were found in the same area on consecutive locations, we marked the location with flagging tape tied to vegetation 2-3 meters on opposite sides of the estimated nest location. Nests were monitored daily to properly assign fates (i.e., hatch, depredated, incubating) and to obtain egg counts when incubating birds were on recess. Hatched nests were determined by the presence of $\geq$ 1 pipped egg in or around the nest bowl.

Brood Capture

All radio-tagged broods were captured when chicks were 11-16 days old. A subset of our broods (resident: n =7, translocated: n = 6) was captured at 4-5 days old then again at 12-13 days old to determine growth rates of northern bobwhite chicks. Location of brooding adults, corral construction, and chick handling methods closely followed the methodology outlined in Smith et al. (2002). However, our design used panels that were 0.9 m tall to prevent escape by chicks with advanced flight abilities as well as any older chicks that could have been adopted by the brooding parent. In addition, we made our cross-member extensions (part that is driven into the ground) 30 cm to provide extra rigidity in looser substrates. In addition to radio-telemetry, we also used a FLIR E-Series forward-looking thermal infrared camera (hereafter, FLIR) (FLIR® Systems, Wilsonville, OR) to aid in locating brooding adults on capture mornings. The FLIR is used to obtain an exact location of the brooding parent and other non-radioed adults by identifying heat signatures of roosted birds. It also reduced pre-mature flushing by the chicks and missing chicks in the corral.

We marked chicks at 4-5 days old according to the methodology outlined in Faircloth et al. (2005). Chicks were weighed using a 30-g Pesola Spring Scale (Pesola AG, Schindellegi, Switzerland). Left wing chord and tarsus were measured with calipers (Anytime Tools, Granada

Hills, CA). We attached patagial wing tags with a unique identification number (National Band & Tag Co., Newport, KY, USA) to the right wing of each chick at 11-16 day old captures. Additionlly, a subset (n ≈ 5) of each brood (11-16 days old) received 0.7-g backpack-style micro-transmitters (American Wildlife Enterprises, Monticello, FL) sutured onto the interscapular region of each chick. Chicks selected for radio attachment had to be at least 14-g with no visible injuries or signs of disease. We used the modified-suture technique (T. Terhune, personal communication) to attach transmitters to all chicks selected for radio attachment. The modified-suture technique is similar to the method described in Burkepile et al. (2002) with some alterations. The modified-suture technique centers the dorsal end of the transmitter at the perpendicular midline of the shoulders (resulting in a lower attachment point than above method); uses smaller needles, suture material, a different knot, and clipped antennas (T. Terhune, pers. comm.). We documented injuries, signs of disease, escaped chicks, and other important observations in the capture records as comments.

We located radio-marked broods 4 times per day. Locations were taken early morning (0700-1000), late morning (1000-1200), early afternoon (1200-1500), and evening (after 1700). Chicks that were located away from their natal brood were found immediately to determine either cause of mortality or adoption by another brood (accomplished by flushing chick). Mortality causes were determined by analyzing evidence discovered at kill site (plucked feathers, chewed transmitter, etc.) (Dumke and Pils 1973).

Landscape Analysis

Digital orthophoto quarter quad tiles (DOQQ) of our study area were acquired from the National Agricultural Imagery Program (hereafter NAIP) (US Department of Agriculture 2017). These DOQQs (1-m spatial resolution raster images) were then combined into a continuous raster image using the mosaic tool in Google Earth Engine (Gorelick et al. 2017). Once the data were combined into 1 continuous image, the Normalized Difference Vegetation Index (hereafter NDVI) was calculated for the entire study area using the NDVI processing tool in the Image Analysis window of ArcMap 10.5 (Environmental Systems Research Institute, Redlands, California, USA). We evaluated the effect of vegetation structure on chick survival at third-order resource selection by estimating home ranges of each chick. We used the dBBMM package in R (R Developemnt Core Team, Vienna, Austria) to calculate 95% home ranges for all chicks with more than 15 locations (n = 87). Once 95% home ranges were calculated, we then used the 'maptools' package in R to create polygons of all home ranges. Home ranges were approximated for chicks with less than 15 locations (n = 22). We found the centroid of each chick's location data using the 'geosphere' package in R, and buffered each centroid by the mean radius of all 95% home ranges calculated for chicks with < 15 locations. We used the 'raster' package to crop and mask the NDVI raster image so that all chick home ranges were individual raster images bound by the spatial extents defined above (home ranges and approximated home ranges). We then averaged NDVI values across each home range and included this average as an individual covariate in our survival models. We evaluated the effect of vegetation structure on chick survival at second-order resource selection by averaging NDVI values at telemetry locations for each chick. Mean NDVI values at chick locations were included as continuous covariates in our survival analysis. Texture measures are based on statistics that describe the spatial relationships between gray tones in an image (Haralick et al. 1973). Texture measures were calculated for our scale of interest (3 x 3 pixel window) by organizing gray tones into a gray-level co-occurrence matrix (GLCM) to compute first and second-order statistics (Hall-Beyer 2007, Wood et al. 2012). Texture measures were calculated using the 'glcm' package in R. We calculated first order statistics (entropy, mean, and, variance) and second-order statistics (homogeneity, contrast, and dissimilarity) for all 95% home ranges and approximated home ranges for all radio-tagged chicks.

Growth Rates

We calculated growth rates for three morphometrics: mass, left wing-chord, and tarsus. Growth rates were obtained by dividing the difference between morphometric measurements at second and first captures by the interval (number of days between captures). We used linear-mixed effects models in the 'lme4' package in R to model differences in offspring growth rates of resident and translocated bobwhites. We also included year as a covariate in this analysis. We also included interaction terms to determine if offspring growth rates varied by group (resident/translocated) or by year. Broods were assigned identification numbers and were included as random effects in our linear models. Effects were not considered significant if 85% confidence limits overlapped zero and if P-values > 0.15.

Survival Estimation

Survival estimates were estimated from the day the first chick entered in the sample (6 Jun) until fall recruitment (1 Oct). Chicks were tracked until fates were determined or were right-censored from the sample. Birds that left the release area, lost due to transmitter failure, or simply disappeared were right-censored from the study sample. We used the known fates model in RMark (Laake and Rexstad 2008) to estimate daily survival rates (DSR), and the logit-link function to restrict survival probabilities between 0 and 1 (Paasivaara and Pöysä 2007).

We included mass, left wing chord length, and tarsus length at second capture as continuous variables in our survival analysis. Individuals with missing morphometric data were assigned mean value of the sample (n = 23). Precipitation data was acquired from a land-based weather station (National Climate Data Center, National Oceanic and Atmospheric Administration, Station ID: GHCND:US1NCBR0061). We used daily summary data (2016 Jun-2016 Oct, 2017 Jun-2017 Oct) to calculate cumulative precipitation and number of significant rain days (> 0.635 cm). Continuous variables were scaled by subtracting the mean of the covariate from each covariate value and dividing by the standard deviation. Age was coded as an individual time-varying covariate but was not scaled to facilitate plotting and interpretation of results.

We used sequential model fitting to help determine the relative importance of covariates based on our candidate hypotheses in each modeling step (Dinsmore et al. 2002, Conkling et al. 2015). Candidate models were organized into 'modeling steps': temporal variation, group effects (translocated/resident), age and morphometrics, precipitation, and NDVI/texture measures. Each model step was composed of candidate hypotheses established *a priori*. The best fitting model was used as a baseline in next model step where new covariates were added based on candidate hypotheses. We began model fitting by including temporal sources of variation (year, linear and quadratic time trends, hatch day) in DSR. The following model steps included intrinsic sources of variation (age, quadratic age, mass, tarsus, and left wing-chord), weather effects (time-varying precipitation, number of days with significant rain events), and landscape effects (Mean home range NDVI, quadratic mean NDVI, and texture measures).

The best approximating models in each modeling step were chosen using Akaike's Information Criterion (AIC_c) and we considered the model with the lowest AIC_c value to be the best approximating model (Burnham and Anderson 1998). We considered similar models if ΔAIC_c values were ≤ 4, granted that models within 4 AIC_c units did not include an uninformative parameter (Burnham and Anderson 2002, Arnold 2010). Relative plausibility of each model was assessed using Akaike weights, w_i (Burnham and Anderson 1998, Anderson et al. 2000), where the best models had the highest Akaike weight. We also reported beta estimates, standard errors, and 85% confidence intervals (CIs) for our top model to improve inference and comparison among covariates (Arnold 2010). We estimated period survival by multiplying DSR estimates generated by our top model by the age range (11-86 days), and other continuous covariates held at their mean values. Period survival estimates were also calculated by year (2016-2017).

RESULTS

Translocations were conducted in 2016 (RA3: 136, RA1: 130) and 2017 (RA4: 128, RA1: 136) with a total of 530 birds across all release areas. We captured 30 bobwhite broods ($n_{Resident}$ = 12, $n_{Translocated}$ = 18) during 2016-2017 and radio-tagged 110 individual northern bobwhites chicks ($n_{Resident}$ = 47, $n_{Translocated}$ = 63) over the 2-year study. Average brood sizes were similar for resident ($\bar{x}$ = 11) and translocated ($\bar{x}$ = 11) bobwhites. In 2016, we radio-tagged 43 bobwhites chicks ($n_{Resident}$ = 13, $n_{Translocated}$ = 30). In 2017, we radio-tagged 67 bobwhite chicks ($n_{Resident}$ = 17, $n_{Translocated}$ = 50). We observed 61 mortalities from 2016–2017. Primary mortality causes were snakes (n = 29, 47.5%), avian (n = 19, 31.1%), unknown (n = 7, 11.5%), mammal (n =5, 8.2%), and weather-related (n = 1, 1.6%). We right-censored 16 individuals (2016: n = 5; 2017: n = 11) from the sample due to the inability to assign fates (Appendix A). We right-censored 15 individuals (2016: n = 5, 2017: n = 10) that were alive at the end of the study. All 109 individuals met our 14 g minimum weight ($\bar{x}$ = 17.2g, range: 14.2–22.5g; Fig. 2). Left wing-chord ($\bar{x}$ = 4.64 cm, 3.65–5.50 cm) (Fig. 3), and tarsus ($\bar{x}$ = 2.15 cm, 1.81–2.39 cm)(Fig. 4) were measured for 86 individuals. Estimates for mean cumulative rain ($\bar{x}$ = 16.2 cm, 0.0–60.8 cm) and significant rain days ($\bar{x}$ = 4.9 days, 0–19 days). Average home ranges did not differ between resident (x = 18.2 ha, 85% CI 16.0–20.4 ha) and translocated (x = 14.6 ha, 85% CI 11.6–17.6 ha).

Growth Rates

We measured growth for 72 chicks between 2016 (resident: n = 20, translocated: n = 25) and 2017 (resident: n = 16, translocated: n = 11). We obtained growth rate information from resident offspring (2016: n = 20, 2017: n = 16) and translocated offspring (2016: n = 25, 2017: n = 11) in all release and reference areas. We measured mass (Fig. 5), tarsus, and left wing-chord growth rates across the 2-year study. Mass growth rates were similar between 2016 (resident = 0.43–1.77 g/day, SD = 0.29, translocated = 0.31–1.18 g/day, SD = 0.23) and 2017 (resident = 0.66–1.52 g/day, SD = 0.21, translocated = 0.45–1.02 g/day, SD = 0.20). Tarsus growth rates were also similar over the 2-year study (2016: resident = 0.02–0.06 cm/day, SD = 0.01, translocated 0.01–0.09 cm/day, SD = 0.02 & 2017: resident = 0.03–0.06 cm/day, SD = 0.01, translocated = 0.02–0.05 cm/day, SD = 0.01). We also didn't find any differences in left wing-chord growth rates in 2016 (resident = 0.28–0.40 cm/day, SD = 0.04, translocated = 0.16–0.49 cm/day, SD = 0.08) and 2017 (resident = 0.25–0.42 cm/day, SD = 0.04, translocated = 0.23–0.41 cm/day, SD = 0.05).

Our top model ($\beta_{\text{Translocated}}$) determined mass growth rates differed between offspring of resident and translocated bobwhites. Mass growth rates in offspring of translocated bobwhites were lower than offspring of resident bobwhites ($\beta_{\text{Translocated}}$ = –0.353, 85% CI (–0.590, –0.117). Model results did not indicate that wing and tarsus growth rates varied by year or between translocated and resident offspring.

Chick Survival

Our most parsimonious temporal-effects model included the effect of year (Table 1); this model was 1.73 times more likely than our second-best model. Our second-best model ($\beta_{Year} + \beta_{Time}$) did receive some support (ΔAICc = 1.1; Table 1), but linear time was an uninformative parameter. However, other models in this step were not competitive based on ΔAICc values. Adding group effects to this model did not improve model fit. The group effects model (translocated) did receive substantial support (ΔAICc = 0.302, Table 1); however, beta estimates overlapped zero indicating that offspring survival rates of translocated and resident adults did not differ. We added release area (Control, RA1, RA3, RA4) as a grouping variable, but did not observe any spatial variation in chick survival across our study site (Figure 6).

Adding intrinsic covariates to the temporal model improved model fit. The top model ($\beta_0 + \beta_{Year} + \beta_{Age} + \beta_{QAge} + \beta_{Tarsus}$) in this step included the effect of age (β_{Age} = -0.011, [85% CI = -0.02–-0.003]), quadratic age (β_{QAge} = 0.0003, [85% CI = 0.0001–0.0004]), and tarsus (β_{Tarsus} = 0.27, [85% CI = 0.09–0.45]). Weather covariates did not improve model fit and competing models included uninformative parameters. NDVI and texture measures also did not improve model fit. Models with the addition of NDVI (ΔAIC_c = 1.01), entropy (ΔAIC_c = 1.72), homogeneity (ΔAIC_c = 1.99), and first-order mean (ΔAIC_c = 1.99), did receive some support but were uninformative. The period survival for bobwhite chicks in 2016 was 0.27 (85% CI = 0.02–0.59) and 0.10 (85% CI = 0.00–0.54) in 2017. Daily survival followed a curvilinear pattern with the lowest survival occurring at about <21 days then slowly increased each day (Fig. 7 and Fig. 8).

DISCUSSION

Our results indicate that annual variation (i.e., year effects) had the strongest influence on survival rates. The site familiarity hypothesis was not supported as offspring of translocated birds had similar survival rates as resident bobwhites. Our hypotheses related to morphometrics did indicate that advanced growth in the first 2 weeks of life increased survival rates of bobwhite chicks. In addition, inclusion of linear and quadratic age covariates indicate there is a curvilinear relationship between age and survival rates of bobwhite chicks with DSR increasing after 20 days in age. The effects of weather and habitat conditions were inconsequential.

Offspring survival rates of translocated and resident bobwhites did not differ across both years of our study, indicating that bobwhites can successfully reproduce and raise offspring after translocation. The recent success of translocation projects offer some evidence that bobwhites can be translocated to new environments and successfully survive and reproduce where sufficient habitat is available (Jones 1999, Liu et al. 2000, Terhune et al. 2006*a*, *b*, 2010). However, the period survival estimates may be biased low (for offspring of resident and translocated bobwhites) in comparison to other studies (Suchy and Munkel 2000, Lusk et al. 2005) suggesting there may be short-term impacts of capture and radio-attachment on bobwhite chicks. Survival estimates that are biased low may be the result of sublethal effects of capture/handling and radio attachment on bobwhite chicks. Capture-related mortalities are often attributed to alterations in behavioral and physiological characteristics of animals post-release (Cox and Afton 1998, Nicholson et al. 2000, Ponjoan et al. 2008). Nonetheless, any bias in survival rates appear to be constant among groups and likely does not affect inference regarding group effects.

We did find annual variation in bobwhite chick survival, which is similar to other species with precocial offspring (Erikstad and Andersen 1983, Paasivaara and Pöysä 2007, Ludwig et al. 2010). Differences in habitat suitability and predator populations in areas selected for translocation in 2016 (RA3) and 2017 (RA4) may have caused annual variation in chick survival during our study. Functional (prey switching) and numerical responses (increased populations) of predators to increasing bobwhite populations (2016: 0.47 bobwhites/ha to 2017: 0.70 bobwhites/ha) on our study area may explain yearly fluctuations in chick survival (Kenward et al. 1981, Hudson and Rands 1988, Salamolard et al. 2000). Annual variations in the timing of precipitation patterns may also explain variation in DSR of bobwhite chicks. Rainfall in June (peak hatch month) was higher in 2017 (17.0 cm) than 2016 (7.6 cm). Increased rainfall may have caused direct mortality due to hypothermia (Stoddard 1931, Spiers et al. 1985, Lusk et al. 2005) or suppression of foraging behaviors during a critical period (Theberge et al. 1973, Pedersen and Steen 1979, Erikstad and Spidsø 1982, Erikstad and Andersen 1983, Ludwig et al. 2010).

Daily survival of radio-tagged chicks (resident and translocated) increased at 20 days in age and maintained a steady increase over time. We expected this relationship because of the development of adult-like flight, increased thermoregulatory abilities (Borchelt and Ringer 1973), and predator recognition as bobwhite chicks age. Mass growth rates were higher in offspring of resident bobwhites (Fig. 5) lending some support to the site familiarity hypothesis. Higher mass growth rates in the offspring of our reference population may be due to the presence of genetics of previously released captive-reared bobwhites (5000 released from 2012–2014). . Our hypotheses related to morphometric effects on chick survival indicated that advanced tarsal development positively affected survival rates. Early tarsal development may portend that increased mobility in flightless chicks may positively impact survival rates to fledging through enhanced foraging and escape abilities. Larger offspring have higher survival rates in several waterfowl species with precocial young (Owen and Black 1989, Schmutz 1993, Traylor and Alisauskas 2006) and in birds with altricial young (Magrath 1991, Linden et al. 1992). The lack of influence of body size and wing growth (prior to capture) on survival rates in our study population may suggest that these morphometrics have little effect of individual fitness in our population (Gebhardt-Henrich and Richner 1998). Future research should seek to identify more important morphometrics (like tarsus length) that may influence survival rates of bobwhite chicks. Individual growth rates may not be the most important factor driving chick survival rates in translocated populations.

Weather did not impact bobwhite chick survival in our study. Although, weather effects on chick survival have been documented in black grouse (*Tetrao tetrix*) and willow ptarmigan (*Lagopus lagopus lagopus*) (Pedersen and Steen 1979, Erikstad and Andersen 1983, Ludwig et al. 2010), these species dealt with colder temperatures in addition to precipitation events which in combination would limit foraging opportunities due to the lack of thermoregulatory ability in young chicks. Direct mortality due to severe rain events has been observed in ring-necked pheasants (Schmitz and Clark 1999) and northern bobwhites (T. Terhune, personal communication). However, bobwhite chicks in the southeastern United States experience relatively warm summer temperatures that may negate or minimize the influence of heavy precipitation. Our selection of 0.635 cm may have not been representative of precipitation levels that impact bobwhite chick survival. Heavy rainfall events may also influence survival rates of bobwhite chicks prior to ages we began radio-tagging individuals when thermoregulatory abilities and thermal insulation (plumage) are less developed (Spiers et al. 1985). Annual fluctuations in weather may limit the reproductive success of translocated bobwhites if heavy rainfall occurs during critical time periods throughout the breeding season (e.g. during the week of peak hatch). Future research with regards to precipitation should aim to determine how timing and severity of precipitation events influence survival, movement behavior, and growth rates of bobwhite chicks.

Satellite imagery of our study area revealed that areas devoid of cover still remained in areas despite having undergone 5 years of intensive habitat management. However, we failed to detect an influence of vegetation structure as measured through NDVI indicating vegetation structure at the scale measured may not affect bobwhite chicks. Landscape composition and configuration did not affect survivorship of pheasant chicks in Iowa, however, survival rates were more variable on the study area with lower grassland cover (Riley et al. 1998). Mortality rates of common goldeneye (*Bucephala clangula*) were not affected by movement through an inhospitable matrix suggesting that factors other than habitat quality may drive offspring survival in precocial young such as spatial distribution of predator populations (Poysa and Paasivaara 2006). Perceptual errors, ecological traps, and threshold effects remain as potential barriers to translocation success (Gilroy and Sutherland 2007, Martin et al. 2017). Further research is needed to better understand the progression of habitat quality at multiple scales for bobwhite chicks post-restoration as we only focused on a single scale in our study.

MANAGEMENT IMPLICATIONS

Short- and long-term evaluations of reintroduction success depends on obtaining accurate parameter estimates post-release. We provide the first estimates of survival for bobwhite chicks post-translocation. These parameter estimates can help population ecologists project population growth post-release, and determine if reintroduced populations will achieve long-term persistence. In addition, we provide the first comparison of chick survival rates between resident and translocated bobwhites post-release. These vital rates provide a measure of how well translocated bobwhites are able to reproduce and raise offspring compared to residents after release. Managers and stakeholders may use these data to help determine: 1) the number of bobwhites to translocate, 2) the number of years to conduct translocations so that desired population responses are obtained, and 3) identify important demographic bottlenecks post-release. We recommend that future research continue to identify important intrinsic (morphmetrics, growth rates, stress hormones, etc.) and extrinsic factors (predator activity, habitat configuration, invertebrate food abundance, etc.) that may limit offspring survival rates of translocated bobwhites post-release.

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Associate Editor:

Figure 1. The study site located in Brunswick County, NC, US. The release areas are denoted by labels on map.

Figure 2. Mass (g) measurements (*n* = 109) of northern bobwhite chicks (*Colinus virginianus*) captured on a private plantation in Brunswick County, NC, USA 2016-2017. Median mass values are indicated by dark centerlines in the box plot, 75% upper quartiles are represented by upper bounds of each box and 25% low quartiles are represented by the lower bounds of each box plot. Points are raw data that are color-coded by brood.

Figure 3. Left wing-chord (cm) measurements of northern bobwhites chicks (*Colinus virginianus*) captured on a private plantation in Brunswick County, NC, USA 2016-2017. Median left wing-chord measurements (*n* = 86) are indicated by dark centerlines in the box plot, 75% upper quartiles are represented by upper bounds of each box and 25% low quartiles are represented by the lower bounds of each box plot. Points are raw data that are color-coded by brood.

Figure 4. Tarsus (cm) measurements of northern bobwhite chicks (*Colinus virginianus*) captured on a private plantation in Brunswick County, NC, USA 2016-2017. Median tarsus measurements (*n* = 86) are indicated by dark center lines in the box plot, 75% upper quartiles are represented by upper bounds of each box and 25% low quartiles are represented by the lower bounds of each box plot. Points are raw data that are color-coded by brood.

Figure 5. Mass growth rate measurements (g/day) of northern bobwhite chicks (*Colinus virginianus*) captured on a private plantation in Brunswick County, NC, USA 2016-2017. Median tarsus measurements (*n* = 72) are indicated by dark center lines in the box plot, 75% upper quartiles are represented by upper bounds of each box and 25% low quartiles are

represented by the lower bounds of each box plot. Points are raw data that are color-coded by brood.

Figure 6. Model-predicted DSR (color-coded by release area) and 85% confidence limits (bars) of northern bobwhite chicks (*Colinus virginianus*) across each release area on a private plantation in Brunswick County, NC, USA 2016–2017.

Figure 7. Top model predicted DSR (solid black line) and 85% confidence limits (shaded area) across observed age values of northern bobwhite chicks (*Colinus virginianus*) on a private plantation in Brunswick County, NC, USA, 2016.

Figure 8. Top model predicted DSR (solid black line) and 85% confidence limits (shaded area) across observed age values of northern bobwhite chicks (*Colinus virginianus*) on a private plantation in Brunswick County, NC, USA, 2017.

Figure 9. Exposure periods (*n* = 43) for all radio-tagged northern bobwhite chicks (*Colinus virginianus*) captured on a private plantation in Brunswick County, NC, UDA, 2016. Fates are color coded by chick (red = mortality, black = censor). The vertical line is 1 Oct 2016 when all chick were right-censored from the study.

Figure 10. Exposure periods (*n* = 66) for all radio-tagged northern bobwhite chicks (*Colinus virginianus*) captured on a private plantation in Brunswick County, NC, UDA, 2017. Fates are color coded by chick (red = mortality, black = censor). The vertical line is 1 Oct 2017 when all chick were right-censored from the study.

Table 1. Model selection results for daily survival rates of northern bobwhite chicks (*Colinus virginianus*) based on sequential model fitting, Brunswick County, NC, USA, 2016-2017.

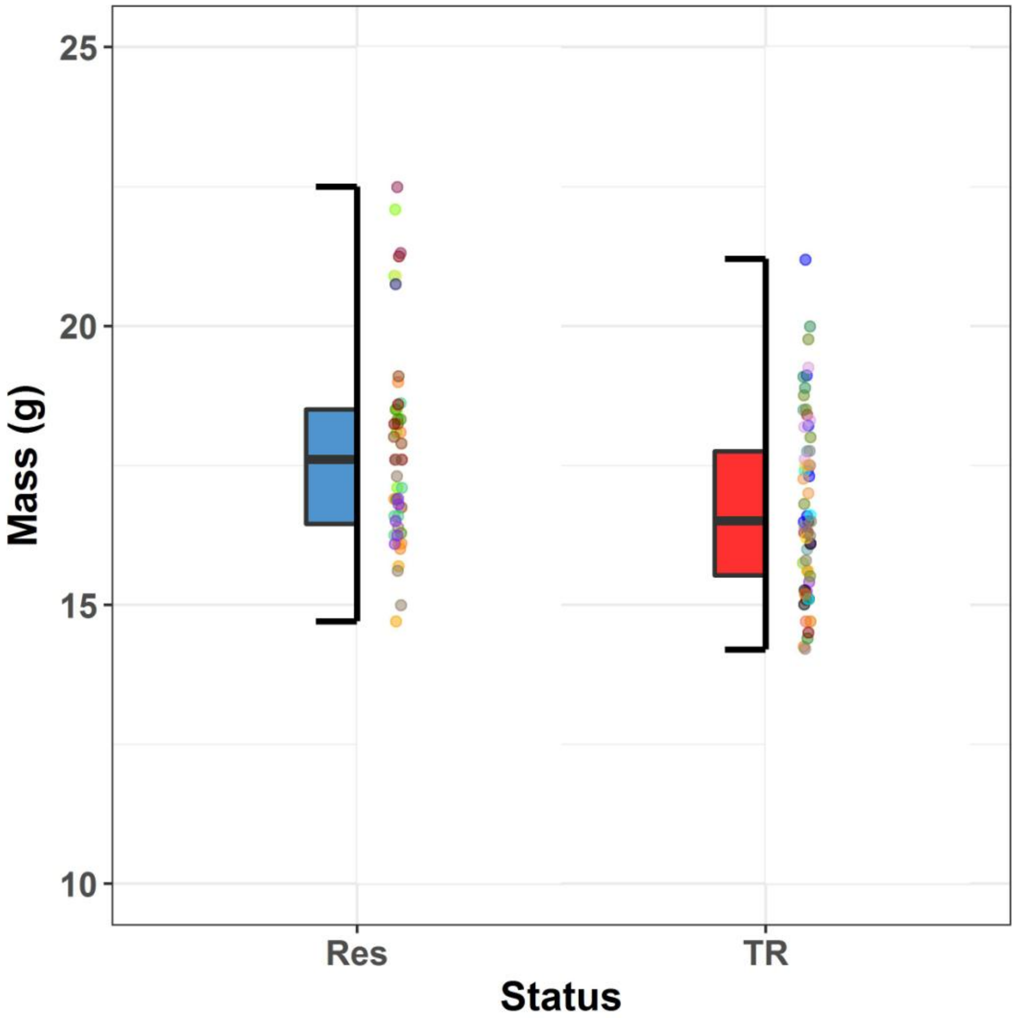
Model	AICc	ΔAICc	w_i	k	Deviance
Temporal Variation					
Year	583.4	0	0.4	2	574.0
Year + Time	584.5	1.1	0.2	3	578.4
Year + QTime[a]	584.9	1.5	0.2	4	576.9
HatchDay	589.8	6.4	0.0	2	585.8
Time	590.7	7.3	0.0	2	228.5
QHatchDay[a]	591.8	8.4	0.0	3	585.8
QTime[a]	591.9	8.5	0.0	3	227.7
Group					
Year	583.4	0	0.5	2	579.3
Year + Translocated	583.7	0.3	0.4	3	577.6
Age and Morphometrics					
Year + QAge[a] + Tarsus	571.2	0	0.6	5	561.2
Year + QAge[a]	574.0	2.7	0.1	4	566.0
Year + QAge[a] + Mass	575.5	4.2	0.0	5	565.5
Year + QAge[a] + LWC	575.8	4.6	0.0	5	565.8
Year + Tarsus	580.0	8.8	0.0	3	574.0
Year + Age + Tarsus	582.0	10.8	0.0	4	574.0
Year	583.4	12.1	0.0	2	579.3
Year + Mass	584.5	13.2	0.0	3	578.5
Year + LWC	585.0	13.8	0.0	3	579.0
Year + Age	585.3	14.1	0.0	3	579.3
Year + Age +Mass	586.5	15.2	0.0	4	578.5
Year + Age + LWC	587.0	15.8	0.0	4	579.0

Weather Effects					
Year + QAge[a] + Tarsus	571.2	0	0.5	5	561.2
Year + QAge[a] + Tarsus + Precip	572.7	1.5	0.2	6	561.7
Year + QAge[a] + Tarsus + SigRain	573.1	1.9	0.2	6	561.1
Year + QAge[a] + Tarsus + Precip*Age	574.8	1.9	0.1	7	560.7
Landscape Variables					
Year + QAge[a] + Tarsus	571.2	0	0.2	5	561.2
Year + QAge[a] + Tarsus + NDVI2	572.2	1.0	0.1	6	560.2
Year + QAge[a] + Tarsus + Entropy	572.9	1.7	0.0	6	560.9
Year + QAge[a] + Tarsus + NDVI3	573.1	1.8	0.0	6	561.0
Year + QAge[a] + Tarsus + HomGen	573.2	1.9	0.0	6	561.2
Year + QAge[a] + Tarsus + Variance	573.2	1.9	0.0	6	561.2
Year + QAge[a] + Tarsus + Mean	573.2	1.9	0.0	6	561.2
Year + QAge[a] + Tarsus + Dissim	573.2	2.0	0.0	6	561.2
Year + QAge[a] + Tarsus + Contrast	573.2	2.0	0.0	6	561.2
Year + QAge[a] + Tarsus + QNDVI	574.0	2.8	0.0	7	560.0
Year + QAge[a] + Tarsus + NDVI*Translocated[b]	575.0	3.8	0.0	8	559.0

[a] Quadratic term includes both linear and quadratic coefficients

[b] Models with interactions with interactions contain main effects

Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community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15
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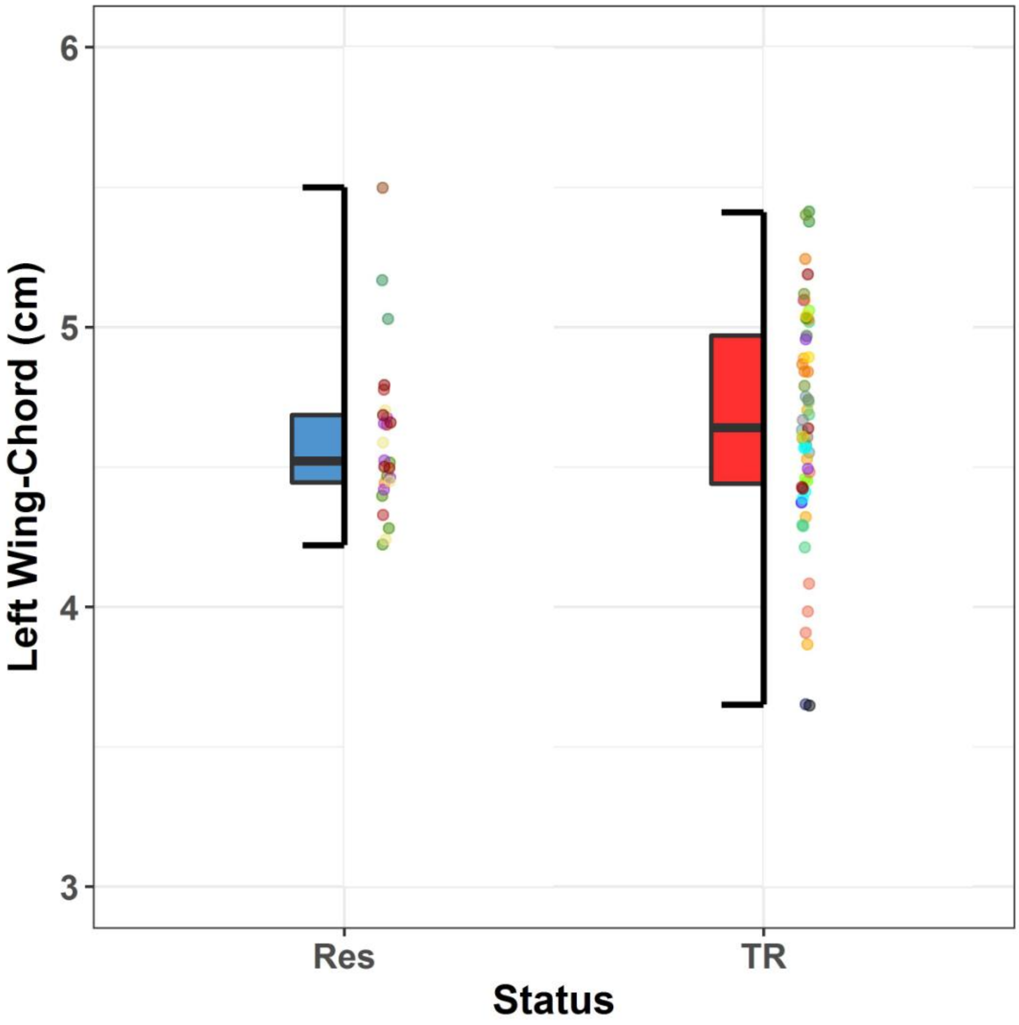
Mass (g)
Res
TR
Status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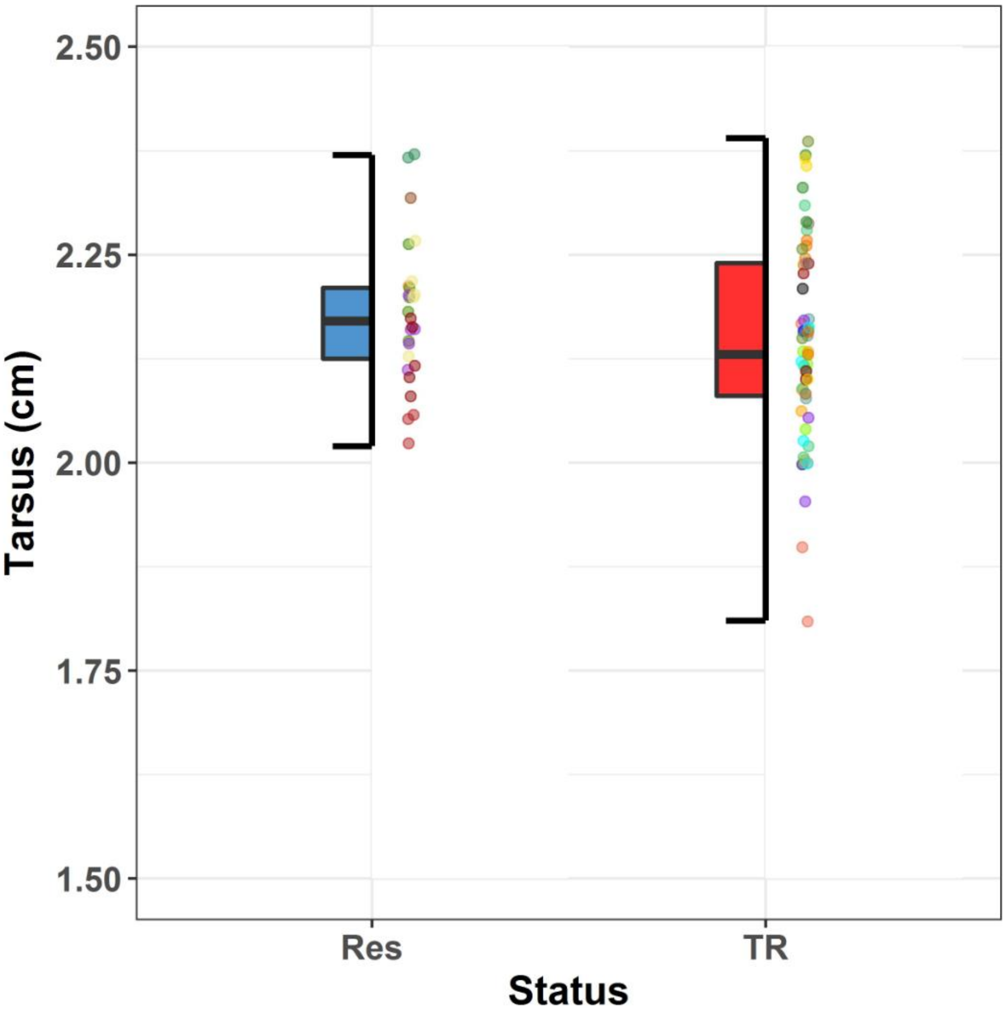
Res
TR
Status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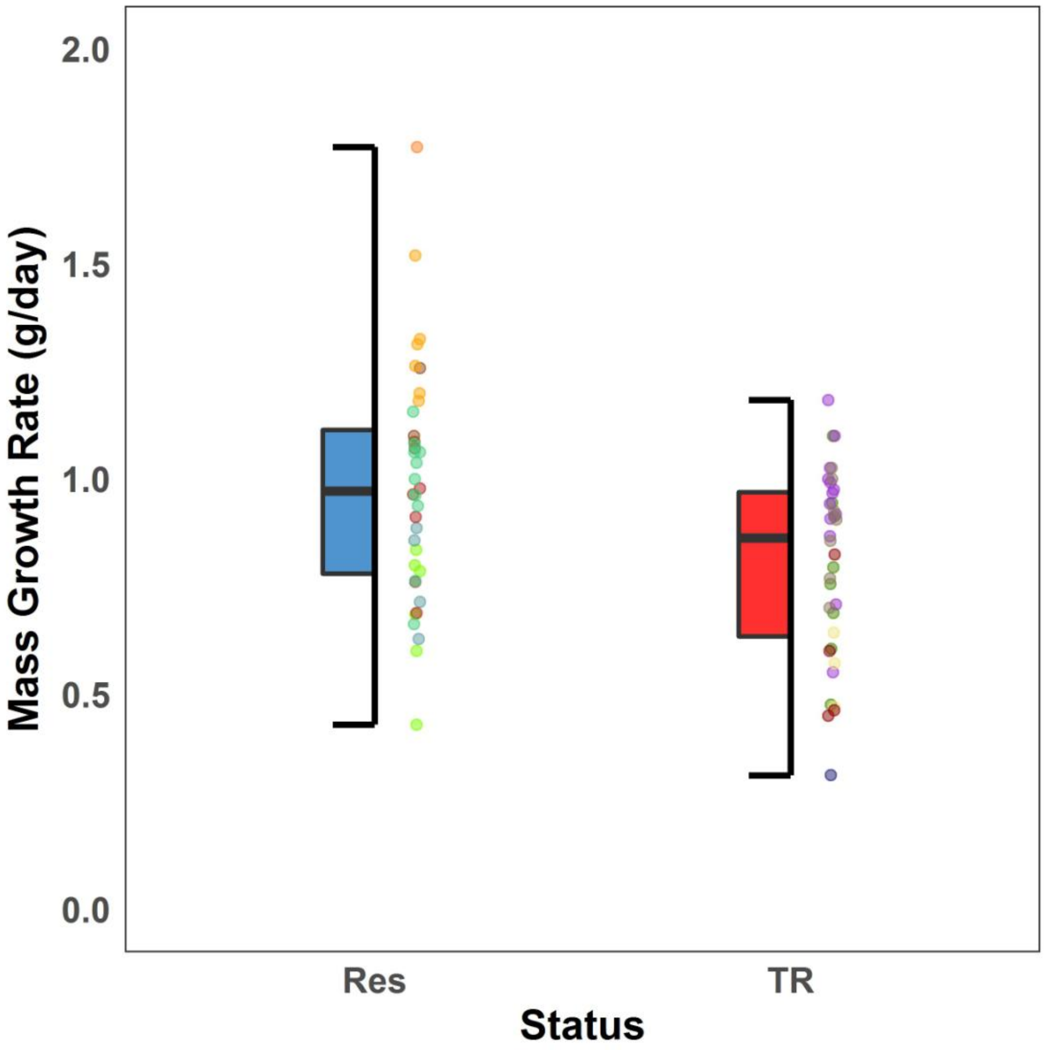
1.75
1.50
Tarsus (cm)
Res
TR
Status



Mass Growth Rate (g/day)
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1.5
1.0
0.5
0.0
Res
TR
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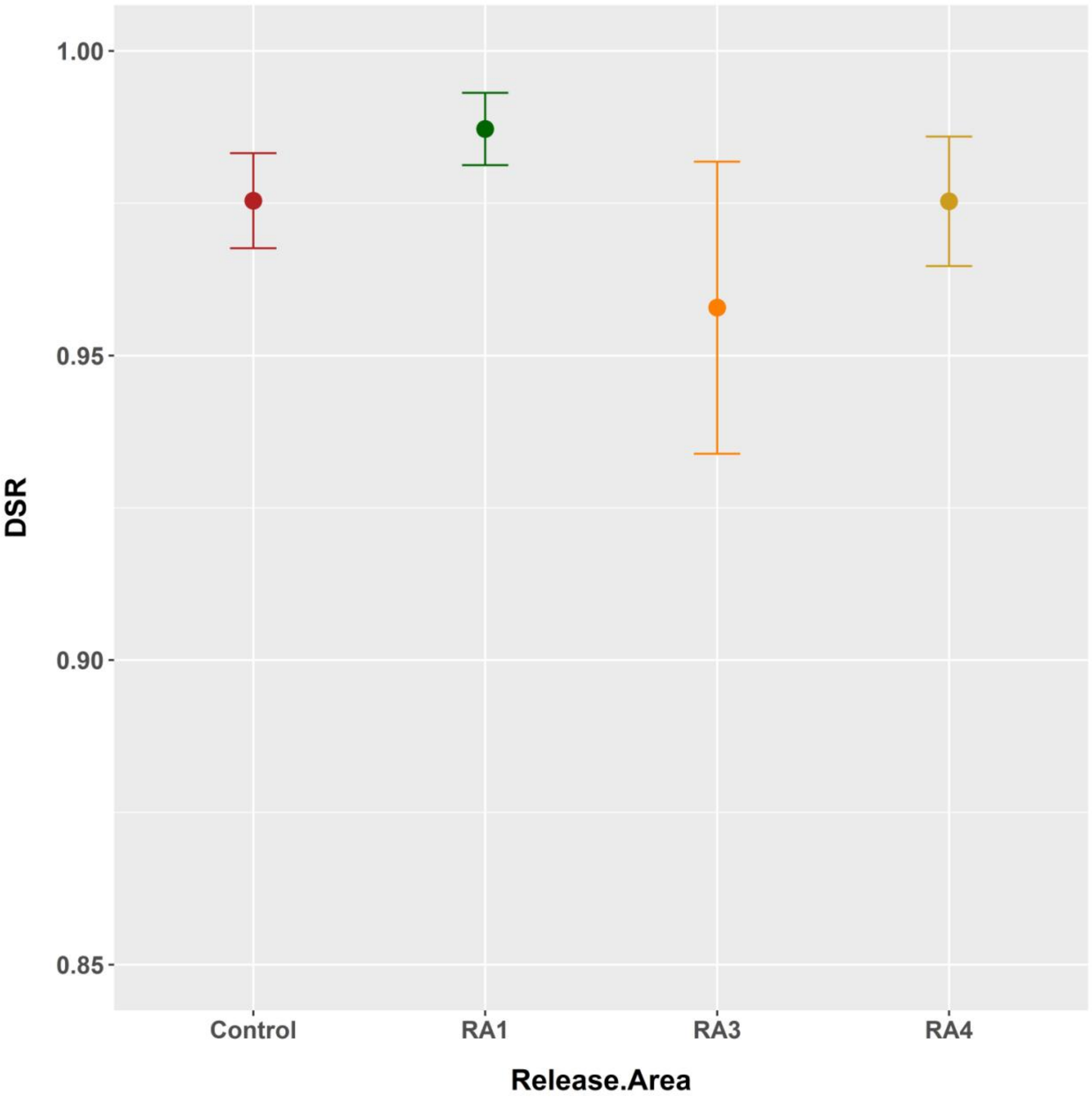
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0.85
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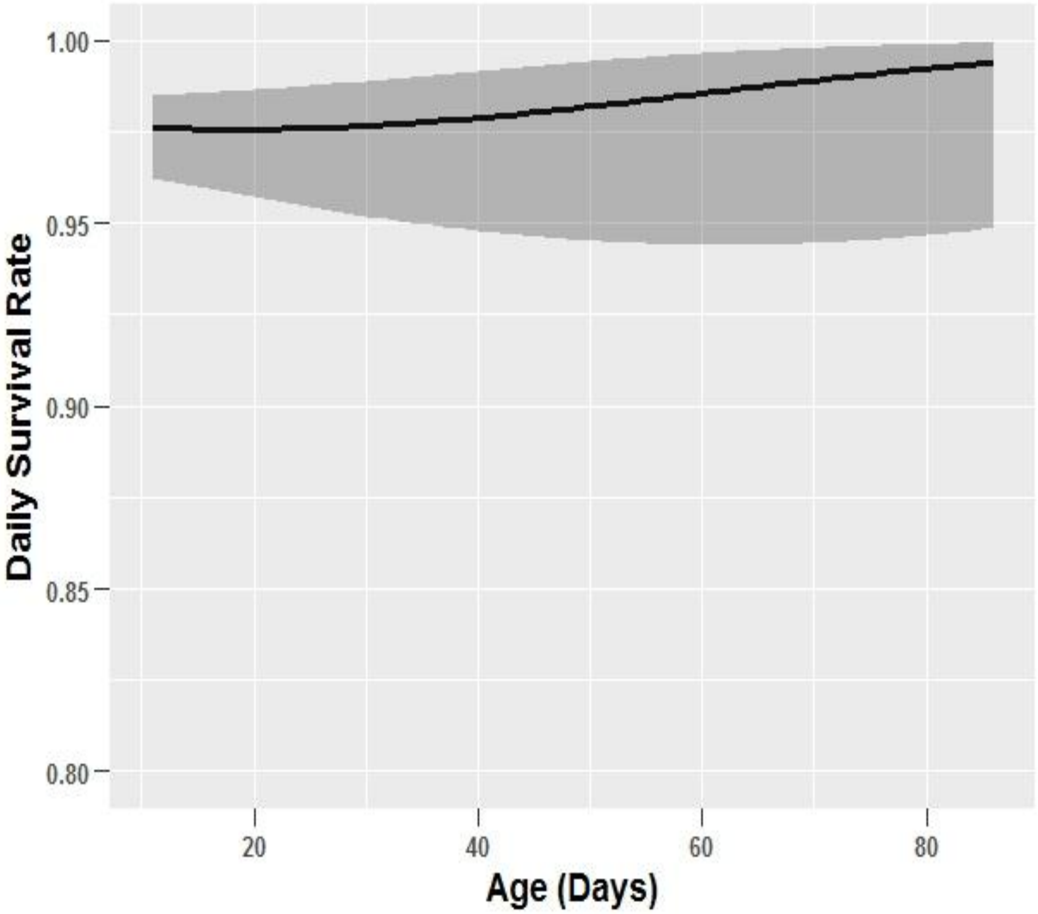
RA3
RA4
Release.Area


Daily Survival Rate
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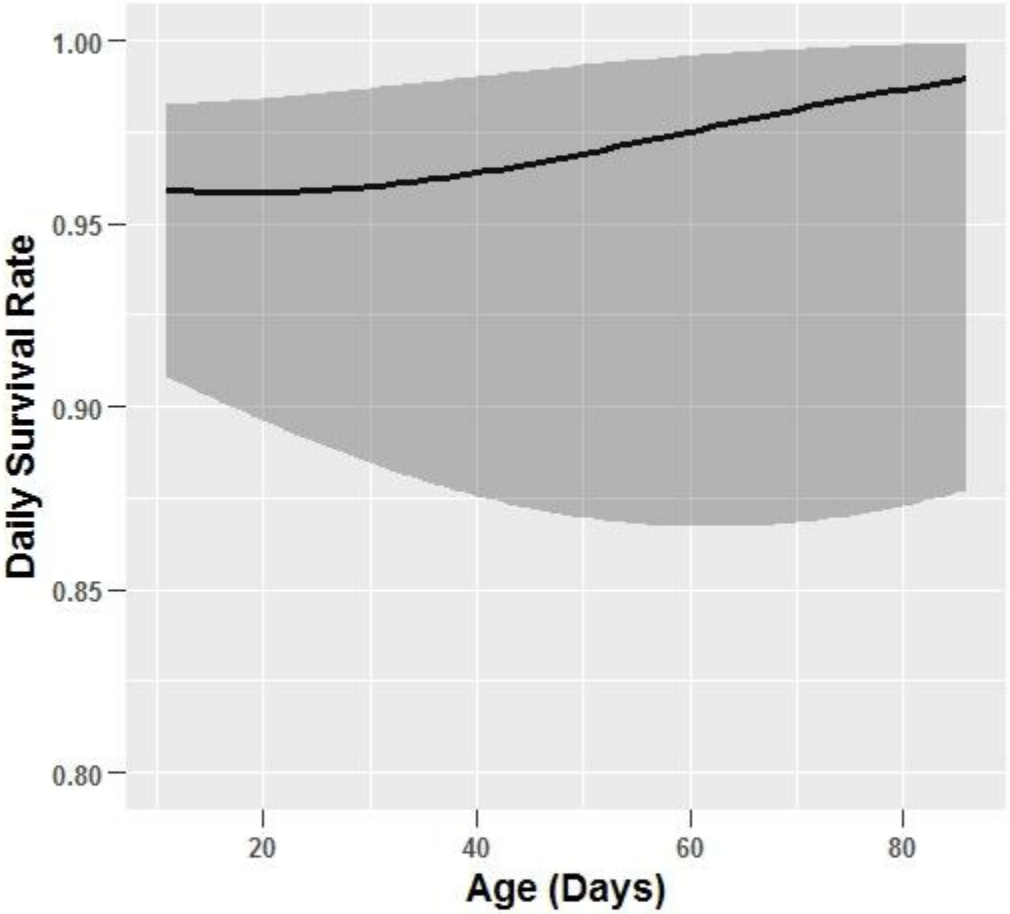
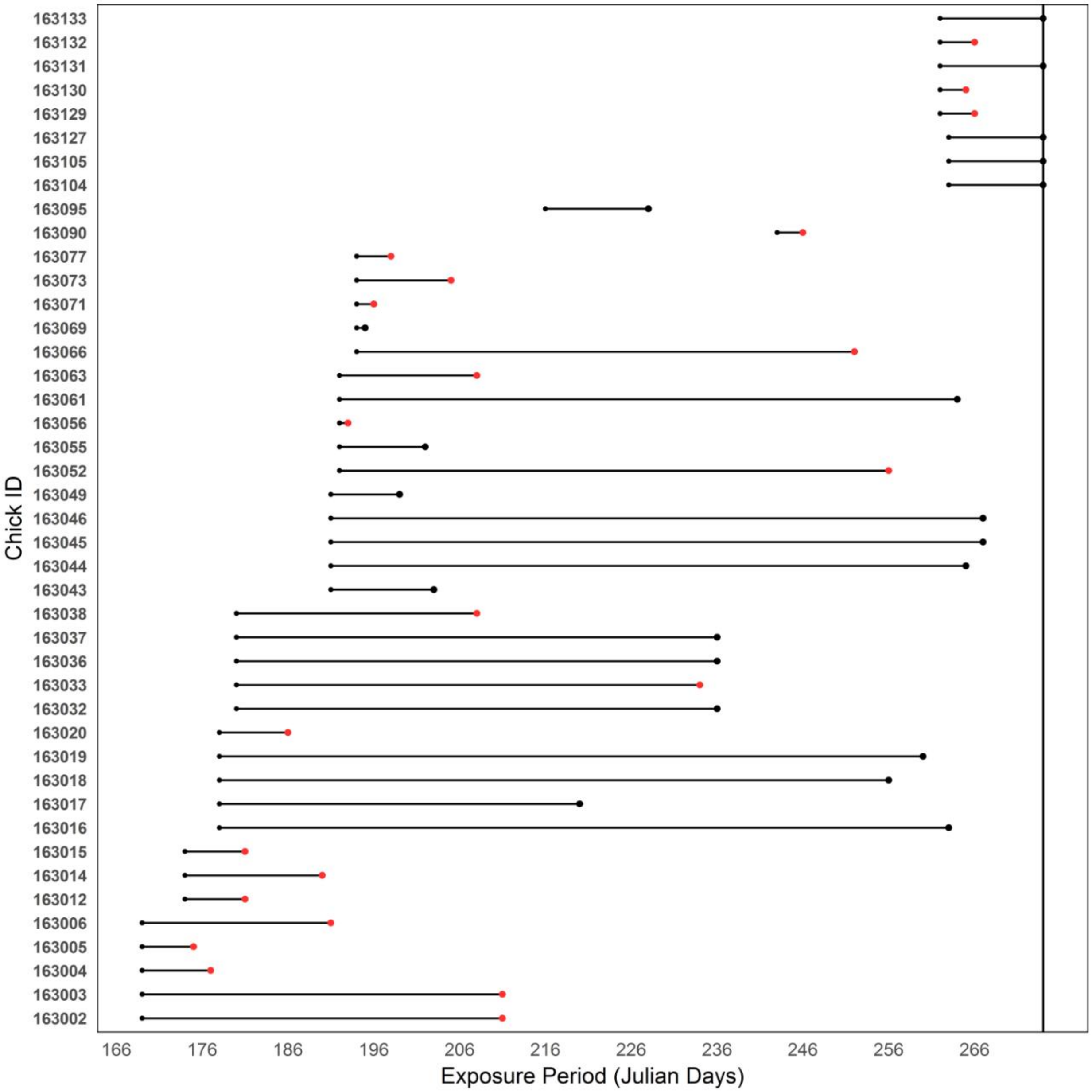
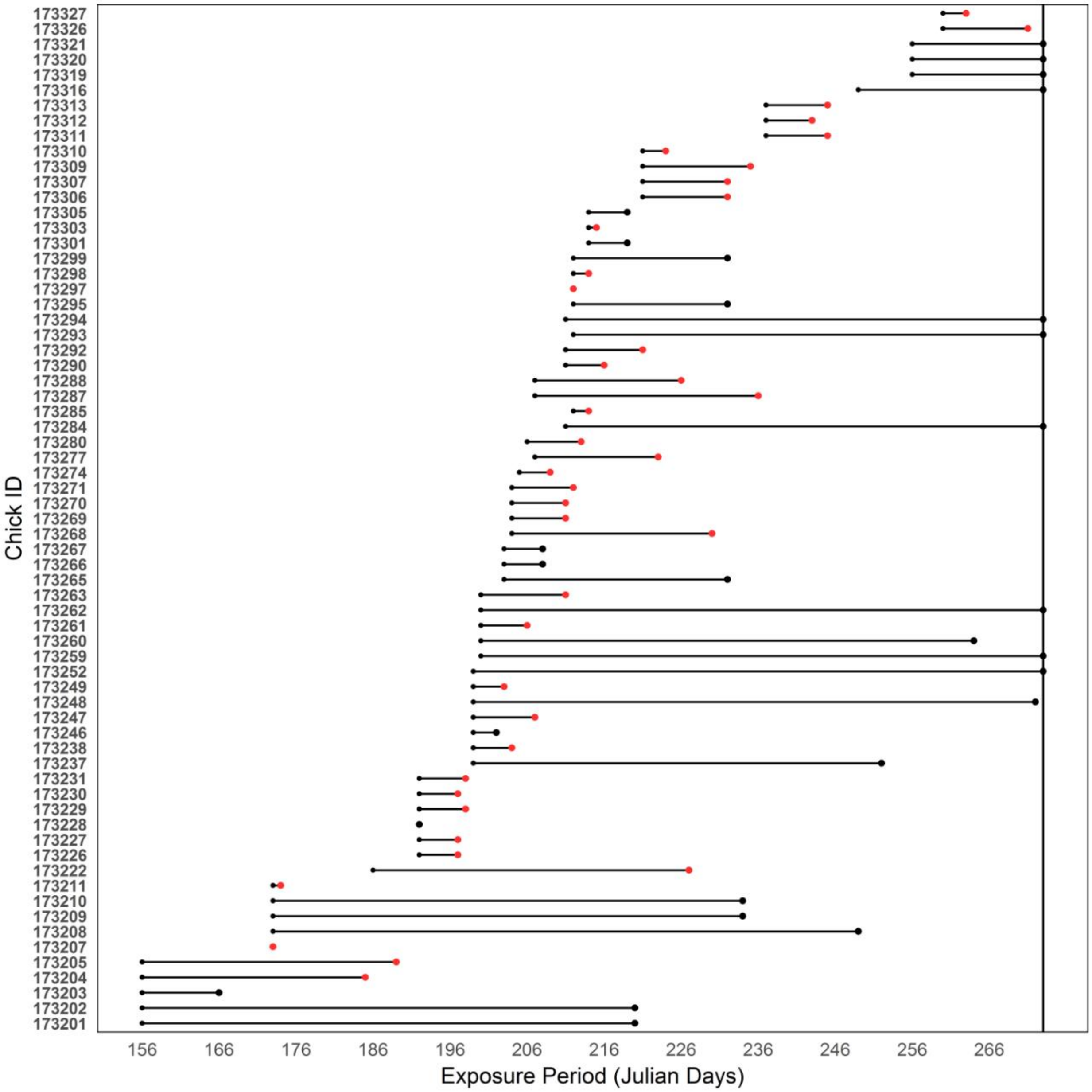
0.95
0.90
0.85
0.80
20
40
60
80
Age (Days)


1.00
0.95
0.90
0.85
0.80
Daily Survival Rate
20
40
60
80
Age (Days)

Summary for online Table of Contents: There were no differences in offspring survival rates of resident and translocated bobwhites post-release. These results suggest that translocated bobwhites are able to successfully reproduce immediately post-release, and contribute to population growth and restoration.

APPENDIX A. LIFESPAN AND EXPOSURE PERIOD INFORMATION FOR NORTHERN BOBWHITE CHICKS

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173227
173226
173222
173211
173210
173209
173208
173207
173205
173204
173203
173202
173201
Chick ID
156
166
176
186
196
206
216
226
236
246
256
266
Exposure Period (Julian Days)

CHAPTER 3

ENVIRONMENTAL AND BEHAVIORIAL FACTORS AFFECT NORTHERN BOBWHITE OFFSPRING SURVIVAL

INTRODUCTION

Parental investment strategies vary across species whereas trade-off decisions allocate parental care between current and future offspring (Williams 1966). Costs of reproduction—reduced survival and foregone future reproduction—may drive variation in parental investment strategies of breeding birds (Dawkins and Carlisle 1976, Reznick 1985). Parental investment is the allocation of resources to behaviors that increase chances of offspring survival while possibly lowering its own survival and future reproductive opportunities (Trivers 1972, 1974). In northern bobwhites (*Colinus virginianus*), parental investment behaviors include finding mates, nest building, egg production, incubation, brooding (offspring thermoregulation), vigilance, and defense/distraction behaviors (Stoddard 1931, Sandercock 1994, Ellis-Felege et al. 2013). Defense behaviors may represent conflicting strategies in brooding adults -- the choice to protect offspring during predator encounters and increase predation risk to themselves or to evade predators and increase their own survival (Andersson et al. 1980, Lima and Dill 1990). These behavioral decisions may carry implications for population dynamics because individual heterogeneity in survival and reproduction can explain population level variations in demography (Gangloff et al. 2018).

Brood defense behaviors are intended to decrease the likelihood of chick mortality and increase one’s fitness (Greig-Smith 1980, Blancher and Robertson 1982, Wiklund 1990). These behaviors are intended to momentarily increase conspicuousness to themselves by diverting the predators focus away from vulnerable offspring and onto the adult(s) (Armstrong 1954, Watson and Jenkins 1964). Nest and brood defense behaviors have been documented in a variety of altricial and precocial bird species and include: calling, fleeing, 'broken-wing' displays, attacks, concealment, altered flights, and altered gaits (Armstrong 1954, Watson and Jenkins 1964, Martin 1984, Knight and Temple 1988, Ellis-Felege et al. 2013). In precocial birds a type of 'broken-wing' distraction display (Armstrong 1954, Hudson and Newborn 1990) attempts to lure predators away from their offspring. As such, decisions regarding the trade-offs between investing in current offspring versus future offspring may be shaped by characteristically long breeding seasons (Roseberry and Klimstra 1984, Burger et al. 1995a).

Bobwhites have a complex mating system (Curtis et al. 1993, Burger et al. 1995) and exhibit flexible reproductive strategies to increase fitness such as varying levels of parental investment or offspring defense. Defense behaviors may operate along a continuum ranging from minimal displays (investment in future offspring) to intense displays (investment in current offspring). Reproductive cost may outweigh perceived predation risk inciting instantaneous parental decisions regarding protection of offspring during predator encounters (Dawkins and Carlisle 1976, Smith 1977, Andersson et al. 1980). Early failure(s) to produce offspring coupled with limited time remaining during the breeding season may elicit riskier behaviors such as defending young. In contrast, long breeding seasons (Klimstra and Roseberry 1975, Roseberry and Klimstra 1984, Burger et al. 1995) may affect individual decisions to defend current offspring early in the season to defer investment to future offspring (within the same season). However, high mortality rates (Burger et al. 1995, Cox et al. 2004, Terhune et al. 2007) jeopardize future reproductive opportunity and may encourage allocation of parental defense to current offspring.

The intersection of parental investment and predation risk underscores the influence that extrinsic factors may have on reproductive success and population growth. The gravity of individual decisions on fitness may be exacerbated by introduction into novel landscapes such that awareness of predation risk and fecundity is relatively diminished in a new environment (Yoder et al. 2004, Kaler et al. 2010). This may be manifested in translocation events where behavior of translocated individuals differ from residents given their past experience(s) or lack thereof (Sih et al. 1998). Successful translocations are predicated on both survival and reproduction, but inexperience with on-site conditions following release may be an impediment for translocated birds to render prudent parental investment decisions, resulting in offspring survival consequences.

Despite bobwhites being one the most studied game birds, scant information currently exists on brood defense behaviors for the species. As such, a goal of this study was to document these behaviors in brood-rearing and to complement known nest defense behaviors for bobwhite (Ellis-Felege et al. 2013). In addition, as part of a larger translocation effort, we evaluated bobwhite offspring defense behaviors for translocated birds compared to resident birds to better understand offspring survival of translocated birds. We predicted that translocation will not affect individual offspring defense behaviors. Although translocated bobwhites were moved across several states (Florida to North Carolina), the suite of predators at both release and donor sites are largely the same indicating similar selective pressures on offspring defense behaviors However, we predicted that brood defense behaviors will impact survival rates of northern bobwhite chicks irrespective of group (translocated, resident). This knowledge will help to inform bobwhite brood ecology, reintroduction biology, and parental investment theory.

STUDY AREA

Our study occurred on a private plantation in Brunswick County, North Carolina, USA. The study site is located in the Carolina flatwoods ecoregion (Griffith et al. 2002). Temperature ranges for Brunswick County, NC are 18°–34° in June through September (National Climate Data Center, National Oceanic and Atmosphere Administration). Average daily rainfall on our study site ranged from 0.63cm (0–20.4cm) per day in 2016 to 0.50cm (0–5.54cm) per day in 2017 (National Climate Data Center, National Oceanic and Atmospheric Administration). Our study site is 2586 ha and contains a mixture of pine flatwoods, savannas, hardwood drains, pocosins, and Carolina bays (Griffith et al. 2002). Pine flatwoods and savannas were predominantly longleaf pine (*Pinus palustris*) with some loblolly pine (*Pinus taeda*) and live oak (*Quercus virginiana*) that were thinned to a basal area of 1.2–2.4 m^2/ha to promote herbaceous understory growth. Understory species in upland areas include wiregrass (*Aristida stricta*), little bluestem (*Schizachyrium scoparium*) and a variety of shrub species including huckleberry (*Gaylussacia spp.),* wax myrtle (*Myrica cerifera*), and gallberry (*Ilex glabra*) The property was used for timber and pine straw and timber production until 2011 when a restoration of longleaf pine-savanna began which included planting of native warm-season grasses, timber thinning, prescribed fire, mowing, hardwood control, supplemental feeding, fallow field management, and meso-mammal trapping (Jackson et al. 2018). All source areas were located in the Red Hills region of northern Florida, and have long practiced intensive habitat management for bobwhites. Managemnt prescriptions of source sites include maintenance of low basal area upland pine forests (e.g. 3–9 m^2 ha^{-1}) dominated by shortleaf (*Pinus echinata*) and loblolly (*Pinus taeda*) pines. Prescribed fire (two-year return interval) and mechanical control (mowing, roller-chopping, herbicide, etc.) are used to maintain early successional vegetation communities such as bunchgrasses (*Andropogon sp.)*, forbs (*Solidago* spp., *Chamaecrista fasciculata*, *Ambrosia artemisifolia*), and blackberry (*Rubus* spp.) Hardwood hammocks/drains and annually disked fallow fields are also interspersed throughout the landscape (Staller et al. 2005, Ellis-Felege et al. 2012, Jackson et al. 2018). Translocation treatments and release area descriptions are also outlined in Lunsford (2018).

METHODS

Capture

Capture and translocation follow the methodologies cited in Lunsford (2018). We captured resident bobwhites during spring (March) and winter (December) trapping periods, 2016 and 2017, using "walk-in" style funnel traps baited with wheat or corn. We used pine limbs to cover traps to provide concealment from avian and mammalian predators, and to reduce stress on captured bobwhites (Terhune et al. 2007). We identified adult/juvenile bobwhites by examining primary coverts (Petrides and Nestler 1943) to locate buff-white tips (indicates juvenile), and inspected superciliary and throat patch coloration to determine sex. We attached 6-g (< 5% body weight) necklace-style radio transmitters (Holohil Systems, Carp, Ontario, Canada) to a subset of captured bobwhites (≥ 132g) after collecting morphometric and demographic information. Trapping methodologies were identical for donor and source sites.

Translocation of bobwhites occurred annually (2016: *n* = 266, 2017: *n* = 270) over the 2-year study from 3 properties in Red Hills region of northern Florida. Two of our source sites were located in Leon County, FL, and the third source site was in Jefferson County, FL approximately 32 km away. Transportation methodology followed protocols outlined in Terhune et al. (2010). Release points at our donor site were located near the centroid of each release area to reduce the chance of individuals leaving the study site.

Telemetry

We tracked bobwhites during the breeding season (1 April - 1 October) at least 2-3 times per week using the homing method (White and Garrott 1990, Kenward 2001). Lotek telemetry receivers (Lotek Wireless, St. Johns, New Foundland, Canada), hand-held 3-element Yagi antennas were used to locate radio-collared bobwhites throughout the study. We kept homing distances to around 25 m to accurately classify habitat information, reduce location bias, and minimize disturbance. We determined nest sites when radio-tagged bobwhites were found in the same area on consecutive locations, and marked them by tying flagging tape to vegetation approximately 2-3 meters on either side of estimated location. Nest sites were checked daily to ensure proper fates (i.e. hatch, depredated, or incubating) were assigned and to obtain egg counts during recess periods of incubating birds. Hatched nests were determined by the presence of ≥ 1 pipped egg in or near the nest location.

Brood Captures

Brood capture, chick data collection, and radio-telemetry methodologies are outlined in Lunsford (2018). Broods of radio-tagged bobwhites were captured when estimated chick ages were 4-6 and 11-16 days. Brood location, corral construction, and chick handling methods were similar to the techniques outlined in Smith et al. (2003). Our corral design used panels that were 0.9-m tall to prevent escape by chicks with advanced flight abilities and older chicks that could have been adopted by the brooding parent. We extended the length of panel cross-members (to 30-cm) to ensure corral rigidity in loose soils and uneven ground at capture sites. Brood locations were usually determined by the use of radio-telemetry, however, FLIR E-Series forward-looking infrared cameras (hereafter, FLIR) (FLIR® Systems, Wilsonville, OR) were used to find exact locations when vegetation structure allowed. The FLIR also helped locate non-radioed adults during brood captures to prevent premature flushing during corral construction (causing a capture failure). We also used the FLIR to locate any missed chicks (e.g. chicks that were hidden in residual vegetation) during brood captures.

We used a 30-g Pesola Spring Scale (Pesola AG, Schindellegi, Switzerland) to measure mass of all captured bobwhite chicks. We measured left wing chord and tarsus lengths with stainless steel calipers (Anytime Tools, Granada Hills, CA). We used permanent markers to assign unique identifiers (color coded markings) to the chin of bobwhite chicks at early (4-6 day captures) brood captures. We used banding pliers to attach patagial wing tags (National Band & Tag Co., Newport, KY, USA) with a unique identification number to the right wing of captured bobwhite chicks at older (11-16 days) captures. We recorded injuries, disease symptoms, escaped chicks, and other important observations in the comments section of capture records. We also documented suspected brood mixing (determined by size and development disparities among offspring and lack of permanent marker colorations) and number of adults present at capture. A subset ($n \approx 5$) was selected to receive backpack-style (0.7 g) micro-transmitters (American Wildlife Enterprises, Monticello, FL). We sutured micro-transmitters onto the interscapular region of chicks using the modified suture technique (T. Terhune, personal communication). This method is similar to the suturing technique used in Burkepile et al. (2002). However, this technique places the dorsal end of transmitter perpendicular to the shoulder midline (lower attachment point), uses smaller needles, suture material, different knots, and trimmed antennas (T. Terhune, personal communication).

Brood Defense

We conducted brood defense encounters when chicks of each brooding bobwhite were 2-4 days old. We performed defense encounters in the late morning to early afternoon to allow vegetation dry out and when no rain was predicted in the immediate (≤ 2-3 hours from encounter time) forecast. These precautions were taken to avoid any mortality associated with hypothermia. We located brooding adults using radio-telemetry and slowly approached the brood until we were in the immediate area.

After brooding adults were encountered, observations and data collection began. Data collected during encounters included: all exhibited behaviors (Table 1), call decision (yes/no), escape decision (yes/no), number of adults present, group (resident/translocated), sex, band ID, radio frequency, and release area. Brooding adults were pursued about 10m from encounter location then observations were ended. If multiple adults were present, we made all efforts to record behaviors of each bobwhite present with the brood. After observations were completed, we immediately documented all behaviors in a written account so observed behaviors and encounter details were recorded accurately. Visibility limitations due to vegetation, multiple adults (displaying in opposite directions, etc.), or other obstacles were noted in the comments after encounters were completed. Once data recording was complete, we immediately left the area so brooding adults could reunite with chicks without further interference. We scaled defense behaviors (Scale: 1 – 7) based on subjective evaluation (observer) of risk/intensity. We summed defense behavior values to create a cumulative score based on all exhibited behaviors of all brood-rearing bobwhites.

We used non-metric multidimensional scaling (NMDS) to explore 'defense behaviors' (Kruskal 1964). Brooding behaviors were coded a "1" if performed during an encounter, or a "0" if they were not. NMDS was used to find correlations among multiple behaviors (n = 7; Table 1) to determine if brooding bobwhites exhibit different behavioral patterns to deter predation. Defense behaviors were analyzed by brood. We used the 'vegan' package in R (R Development Core Team, Vienna, Austria) to create a rank-order dissimilarity-matrix based on pairwise comparisons of defense behaviors to develop correlations (organized by encounters) based on Bray-Curtis distance coefficients. Once dissimilarity matrices are generated, then brooding parents (along with defense behaviors) are randomly placed in ordinal space. Algorithms, ran iteratively, were used to refine the ordinal placement of parents and behaviors until ordinal distances closely match the rank-order distances from the original dissimilarity matrix. We then obtained ordinal values of defense behaviors of each brood-rearing parent. We used the envfit function in the 'vegan' package in R to determine which brood defense behaviors and characteristics significantly ($\alpha = 0.15$) affected ordinations of defense behaviors of brood-rearing bobwhites. We used the 'lm' command in R to analyze differences in ordination scores ($\alpha = 0.15$) of resident and translocated bobwhites to determine if brood-rearing strategies were differed among the two groups, and to determine which covariates predicted 'intensity' of brood defense behaviors. We included day of breeding season, group (resident/translocated), brood size (number of hatched chicks), mass (at spring capture), and age (adult/juvenile) as predictor variables to determine which factors best predicted defense behavior intensity. All continuous variables were scaled to facilitate comprehension of effect magnitudes.

Survival Estimation

Survival estimates were obtained from the first day chicks were radio-tagged until 21 days in age. We selected 21 days as the cut-off age because this is the life stage where adults are still providing parental care, and chicks have not fully developed flight abilities. The lack of adult-like flight abilities limits the chances that chicks can escape during predator encounters making them more vulnerable to mortality. Our exposure period for each radio-tagged chick was the first day it entered the study sample (day of radio-tagging) until 21 days in age. We estimated daily survival rates (DSR) using the known fates model in RMark (Laake and Rexstad 2008), and restricted survival probabilities between 0 and 1 using the logit-link function (Paasivaara and Pöysä 2007).

We included temporal sources of variation, morphometric data, precipitation data, and age information in our survival analysis because they may affect chick survival; these variables were not our main interest but have shown to be informative in previous analyses (Lunsford 2018).

Morphometric measurements (mass, left wing chord, and tarsus) were included as continuous variables in our survival analysis. Mean covariate values were assigned to individuals with missing morphometric data (*n* = 23). We downloaded precipitation data from a land-based weather station (National Oceanic and Atmospheric Administration's National Climate Data Center–Station ID: GHCND–US1NCBR0061). Our daily precipitation data was taken from Jun – Oct, 2016–2017. We used daily precipitation values as time-varying covariates in our survival analysis, and calculated significant rain days (> 0.635 cm) and included it as a continuous variable. We scaled all continuous variables by subtracting covariate means from covariate values, and dividing by the standard deviation. We also coded age as a time-varying covariate, and was not scaled for interpretation of results and to facilitate plotting. Behavioral covariates, subjective intensity score and presence of brooding parent, were included in the final model step to evaluate the effects of parental behavior on chick survival.

We evaluated the relative importance of covariates using sequential model fitting based on a set of candidate hypotheses constructed *a priori* (Dinsmore et al. 2002, Conkling et al. 2015). We organized candidate hypotheses into 'model steps': temporal variation, group effects (translocated/resident), age and morphometrics, precipitation, and behavioral covariates. We used best fitting models from each step as a baseline to construct hypotheses with new covariates. We began model fitting by evaluating temporal sources of variation in DSR of bobwhite chicks (year, hatch day). Additionally, we evaluated intrinsic sources of variation (morphometrics), precipitation (time-varying precipitation, significant rain days), and behavioral effects (defense behavior intensity score, presence of brooding adult) in subsequent model steps.

Our best approximating models were chosen using Akaike's Information Criterion (AIC_c);

models with the lowest $\mathrm{AIC_c}$ values were considered to be best approximating models in each model step (Burnham and Anderson 1998). We evaluated model similarity using $\Delta\mathrm{AIC_c}$ values; values that were ≤ 4 $\mathrm{AIC_c}$ were considered similar granted they did not include an uninformative parameter (Burnham and Anderson 2002, Arnold 2010). Akaike model weights, w_i (Burnham and Anderson 1998, Anderson et al. 2000), were used to evaluate the relative plausibility of each candidate hypothesis with the best model having the highest weight. We reported beta estimates, standard errors, and 85% confidence intervals (CIs) for our top model to facilitate interpretation of effect sizes and comparison among predictor variables (Arnold 2010).

RESULTS

We conducted brood defense encounters on 20 bobwhite broods ($n_{Resident} = 7$, $n_{Translocated} = 13$, $n_{adult} = 8$, $n_{juvenile} = 12$) and radio-tagged 73 individual bobwhite chicks ($n_{Resident} = 25$, $n_{Translocated} = 48$) in 2016-2017. We censored 3 broods ($n_{chicks} = 12$) from the behavior study due to the inability to observe defense behaviors in dense vegetation. Average brood size of resident (SD = 3.03) and translocated (SD = 3.56) bobwhites was 11 chicks. We observed 10 multi-parent broods and 10 single-parent broods during behavioral observations. Ten out of 20 sampled broods were amalgamated based on chin markings and growth disparities (mass, wing length etc.) among chicks. We also recorded broods with multiple adults during brood captures in 2016 ($n_{Resident} = 9$, $n_{Translocated} = 6$) and 2017 ($n_{Resident} = 2$, $n_{Translocated} = 4$).

Defense Behaviors

We did not observe any differences in brood defense behavior of translocated ($\bar{x}$ – NMDS 1: –0.083, NMDS 2:–0.068) and resident bobwhites ($\bar{x}$ – NMDS 1: 0.119, NMDS 2: 0.098) based on ordination of defense behaviors (Figure 1) and linear models (NMDS 1: $P = 0.605$ df = 1, NMDS 2:

$P = 0.437$, df = 1). Our behavioral observations yielded 7 different defense behaviors (Table 1) exhibited by brood-rearing bobwhites: fly away [no defense/distraction attempts, $n = 1$), labored flight ($n = 1$), run ($n = 3$), hold tight ($n = 9$)], labored flight with broken-wing display ($n = 13$), run with broken-wing display ($n = 8$), and approach (approached observer instead of fleeing, $n = 2$). Other behaviors we observed during defense encounters included vocalizations and escape behaviors the immediate area (long distance flight away from brood). We found six brood defense characteristics that predicted ordination of defense strategies of brood-rearing bobwhites; escape (-0.018, -0.999, $P = 0.003$, $R^2 = 0.53$), multiple adults (-0.574, 0.818, $P = 0.001$, $R^2 = 0.77$), approach (-0.630, 0.775, $P = 0.04$, $R^2 = 0.36$), run with broken-wing display (-0.575, 0.817, $P = 0.002$, $R^2 = 0.59$), run (0.851, 0.524, $P = 0.006$, $R^2 = 0.70$), and flutter with broken-wing display (-0.433, -0.901, $P = 0.147$, $R^2 = 0.22$). Only one of our predictor variables affected the intensity of brood defense behaviors, day of breeding season ($\beta_{\text{Day.Number}} = 4.88$, 85% CI 1.66–8.10 $P = 0.05$, $R^2 = 0.195$, df = 5), based on linear models.

Survival Analysis

The most parsimonious temporal effects model was the null model (Table 2) indicating there were no significant time trends in bobwhite chick survival over the study period. Other candidate hypotheses in this model step were competitive ($\leq 4\ \Delta\text{AIC}_c$), however, covariates were considered uninformative based on confidence intervals overlapping zero. Addition of the grouping covariate (translocated/resident) did not improve model fit based on standard error values, indicating that offspring of resident and translocated bobwhites had similar survival rates to fledging. Intrinsic sources of variation (age and morphometrics) did not improve model fit due to uninformative parameters. Inclusion of time-varying precipitation and behavior improved model fit. Defense behavior intensity impacted chick survival. Our most parsimonious model ($\beta_0 + \beta_{\text{Precip}} + \beta_{\text{Intensity}}$)

included effects time-varying precipitation (β_{Precip} = –0.31, 85% CI = –0.45,–0.17) and defense behavior intensity ($\beta_{Intensity}$ = 0.58, 85% CI = 0.14–1.01).

Discussion

We observed a plethora of brood defense behaviors that are consistent with the precocial bird literature. Our results indicate that brood defense behaviors and environmental conditions (i.e., rainfall) influence chick survival before fledging from adults. Aggressive defense behaviors were more common later in the nesting season and in general had positive effects on chick survival. As predicted, rainfall decreased chick survival and our approach highlights the importance of using time-varying weather conditions. Our neutral hypothesis regarding differences in parental investment strategies between resident and translocated bobwhites was supported due to similarities in brood defense behaviors between the two groups. Collectively, our results suggest that variation in behavior, as possibly driven by individual heterogeneity and context (i.e., time remaining in breeding season), coupled with environmental constraints (i.e., too much rainfall) affect survival of precocial young. These inferences contribute to a limited body of literature on precocial birds because most similar work has been done on altricial birds. Additionally, we observed that translocation does not alter parental investment strategies of northern bobwhites indicating that behaviors adapted to reduce juvenile mortality are still expressed in reintroduced populations.

Bobwhites have evolved similar brood defense behaviors as other game birds. Red grouse (*Lagopus lagopus scoticus*), black grouse (*Tetrao tetrix*) and capercaillie (*Tetrao urogallus*) have been observed exhibiting similar brood defense behaviors such as heavy flights, injury flights, crouched runs, circling (short distance flight followed by alert posture), injury feigning, and vocalizations (Watson and Jenkins 1964, Pedersen and Steen 1985, Sonerud 1988). Our observed behaviors such as running with broken-wing display (combination of crouched run and injury-feigning), labored flight with broken-wing display (injury flight), labored flight, and vocalizations were similar to bobwhite nest-defense behaviors reported by Ellis-Felege et al. (2013). The presence of multiple adults may benefit parent and offspring survival due to the dilution of predation risk (Hamilton 1971), and confusion (Miller 1922) of predators with multiple adults displaying distraction behaviors. Ellis-Felege et al. (2013) demonstrated predator-specific risk-assessment during nest-predator encounters (Ellis-Felege et al. 2013). We observed much lower rates of 'no defense' or outright fleeing behavior in brooding adults. Broods represent a successful breeding which may elicit stronger defense behaviors in breeding bobwhites due to energy already invested in finding mates, nest building, incubation, and brood-rearing. Bobwhite chicks have cryptic coloration and are mobile which may increase survival chances when coupled with defense behaviors of brooding adults.

Our discovery that brood defense behaviors for resident and translocated bobwhites did not differ was not unexpected. Natural selection shapes behavioral strategies that confer fitness gains in the context of extrinsic pressures such as environmental constraints and predator interactions (Davies et al. 2012). Similar predator communities between source sites and donor sites may potentially explain the lack of difference in defense behaviors in resident and translocated bobwhites due to taxonomic and functional similarities (foraging patterns and behaviors) in predator species (Sih et al. 1998). This suite of defense behaviors may have been selected for due to their ability to distract a variety predators (avian, mammals, and snakes) that prey on offspring, while minimizing adult predation risk (Andersson et al. 1980). Previous research has shown that bobwhites are able to distinguish between predator species that represent low (small snakes, armadillos, etc.) and high (bobcats, large snakes, etc.) mortality risk and are able to make instantaneous decisions regarding the defense of offspring and maximizing their own survival (Veen et al. 2000, Staller et al. 2005, Ellis-Felege et al. 2013). In addition to species, types of predator encounters may influence behavior decisions in brooding bobwhites. Bobwhites and their broods may be ambushed by predators (predator detects prey first) or the brooding parent may detect predators first provoking various threat levels influencing decisions (Lima and Dill 1990). The ability to process threat-levels may be innate in bobwhites indicating that brood defense behaviors may be similar among populations.

Our results indicate that intensity of defense behaviors impact chick survival in bobwhites. These results imply that risky behavior to defend offspring increases chick survival. Predation was the primary cause of mortality in our study, and included a variety of snake species (*Coluber constrictor, Pantherophis guttatus, Agkistrodon piscivorous*), mammals, and avian predators. A diverse predator community may have produced similar brood defense behaviors among brood-rearing bobwhites considering varying predator strategies such as forage timing (diurnal/nocturnal) and foraging strategies (Ellis-Felege et al. 2013). The evolution of offspring defense behaviors among birds in response to predators (Armstrong 1954, Watson and Jenkins 1964, Davies et al. 2012) may have been learned through previous predator encounters or a direct result of selective pressures from multiple species (Lima and Dill 1990, Davies et al. 2012).

The results of our study have some important caveats. The use of humans to simulate predators during encounters may alter defense decisions in brooding bobwhites due to innate predator responses and previous encounters with humans (Knight and Temple 1986, Montgomerie and Weatherhead 1988, Ellis-Felege et al. 2013). The presence of vehicles, noise from telemetry equipment, and site profiles of observers may have biased defense behaviors by alerting brooding adults to our presence long before encounters began or habituated them to human disturbance over the course of a breeding season. In addition, we only observed defense behaviors early in early life stages, which may amplify defense intensities of adults due to the vulnerability of offspring. Bobwhite chicks at 2-4 days old lack flight capability at this life stage and are not able to thermoregulate without an adult (Borchelt and Ringer 1973, Spiers et al. 1985) making them extremely vulnerable to predators when separated from the parent. Thus, inference from our study should be limited to the early life-stages for chicks. We only observed bobwhites a single time during brooding, however, bobwhites can judge perceived threats based on predator species and adjust their behaviors accordingly (Ellis-Felege et al. 2013). Additionally, subjective scoring of defense behavior intensity may not accurately reflect true risk/intensity of behaviors. Future research should be directed at determining the effect of brood defense behaviors on survival of adult bobwhites, and determining if brood defense behaviors are sex-specific. In addition, future research should also be directed at discovering other anti-predator behaviors of brooding bobwhites, such as spatial avoidance, movement patterns, and vegetative cover use (Sonerud 1985). The on-going evaluation of translocation as a population restoration method needs to continue discovering factors that may limit the success of translocation. Our research here suggests that translocation does not suppress innate behaviors or alter parental investment strategies of bobwhites that are conducive to offspring survival.

DECLARATIONS

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Table 1 Brood defense behaviors exhibited by northern bobwhites (*Colinus virginianus*) during simulated predator encounters conducted on a private plantation in Brunswick County, NC, USA 2016-2017.

Table 2 Beta coefficients from linear modeling of behavioral intensity estimates based on behavioral observations of brood-rearing northern bobwhites (*Colinus virginianus*) on a private plantation in Brunswick County, NC, USA 2016–2017.

Table 3 Model selection results for daily survival rates of northern bobwhite chicks (*Colinus* *virginianus*) based on sequential model fitting of environmental and behavioral variables, Brunswick County, NC, USA, 2016-2017.

Figure 1. Graphical ordination (non-metric multidimensional scaling) of defense behaviors of resident (*n* = 7) and translocated (*n* = 10) northern bobwhites (*Colinus* virginianus) during simulated predator encounters conducted on a private plantation in Brunswick County, NC, USA, 2016-2017.

Figure 2. Graphical ordination (non-metric multidimensional scaling) of defense behaviors of all northern bobwhites (*Colinus virginianus*) during simulated predator encounters (*n* = 17) conducted on a private plantation in Brunswick County, NC, US, 2016-2017.

Figure 3. Model predicted (solid black line) and raw behavioral intensity scores (points) of brood-rearing northern bobwhites (*Colinus virginianus*) and 85% confidence limits (shaded area) across day of breeding season on a private plantation in Brunswick County, NC, USA, 2016–2017.

Figure 4. Top model predicted daily survival rate (DSR) of radio-tagged northern bobwhite chicks (solid black line) and 85% confidence limits (shaded area) across scored defense behaviors of brood-rearing northern bobwhites (*Colinus virginianus*) on a private plantation in Brunswick County, NC, USA, 2016–2017.

Figure 5. Top model predicted daily survival rate (DSR) of radio-tagged northern bobwhite chicks (solid black line) and 85% confidence limits (shaded area) across precipitation (cm) values on a

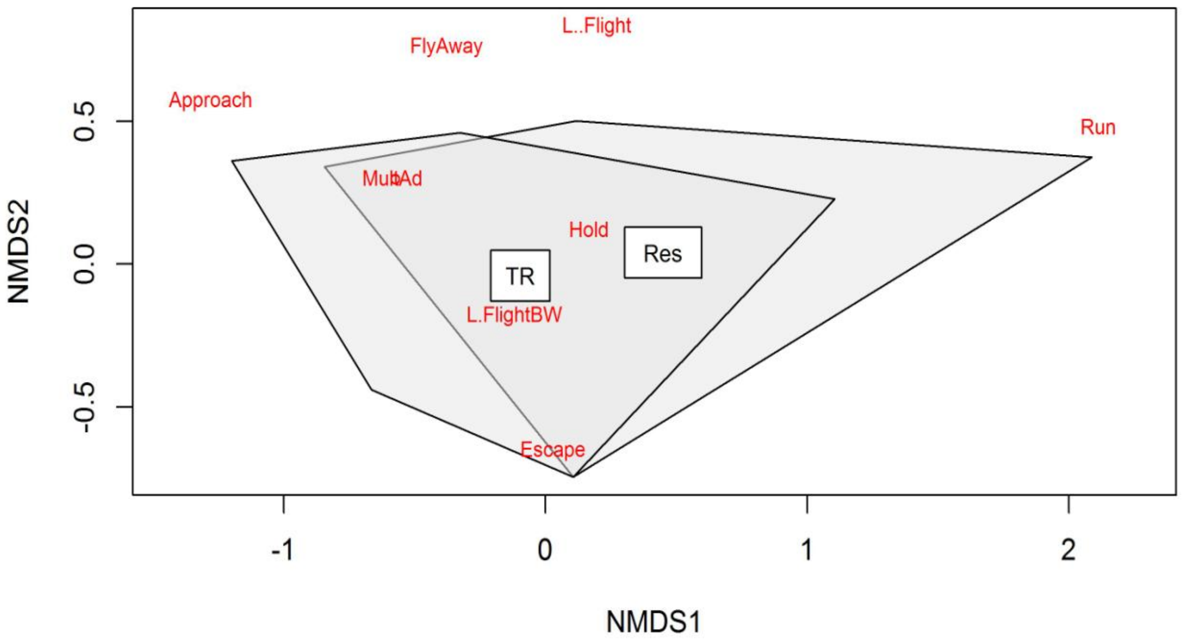
private plantation in Brunswick County, NC, USA, 2016–2017.

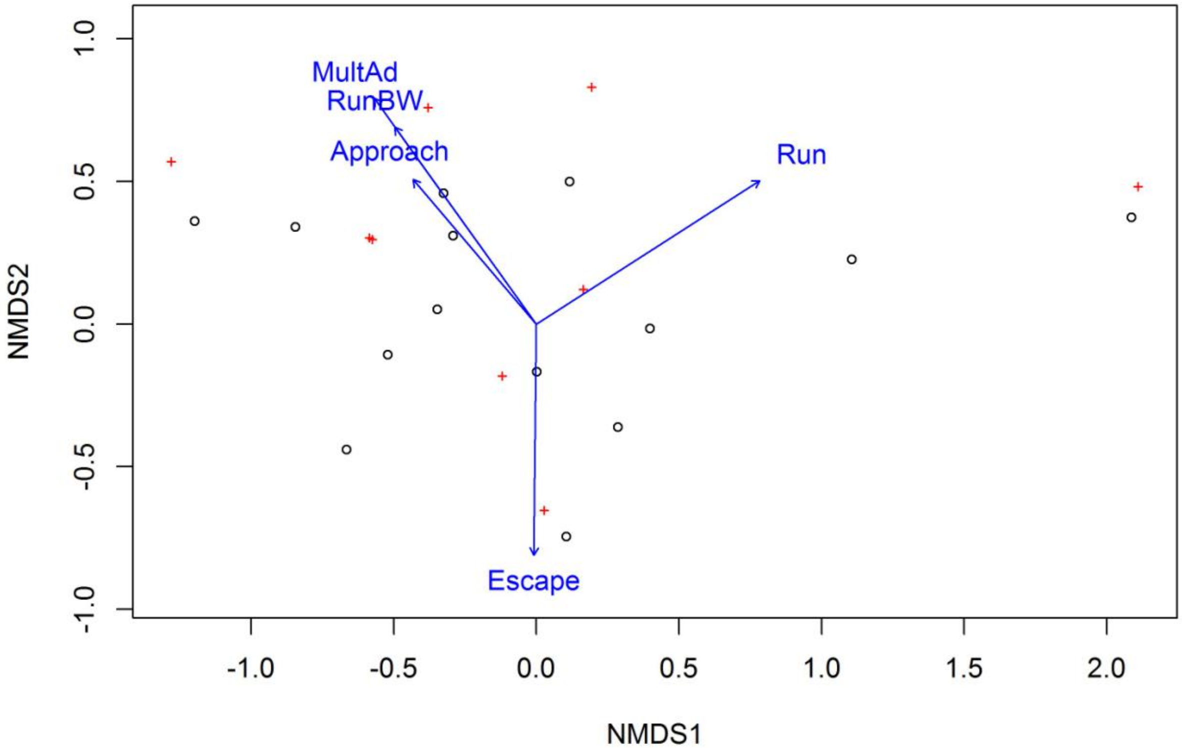
Behavior	**Description**
Run	Parent ran into cover immediately, and did not exhibit any injury-feigning or flight behaviors
Fly Away	Parent flew away from the immediate area of the brood, and exhibited no injury-feigning or distraction displays
Labored Flight	Parent exhibited a short, labored flight, and landed near the encounter area.
Hold	Parent did not exhibit any distraction or defense displays until observer(s) were within 1m of location.
Labored Flight with Broken-Wing Display	Parent exhibited 'Labored Flight' behavior described above, while exhibiting the injury-feigning 'broken-wing' display.
Run with Broken Wing Display	Parent went into a labored run while exhibiting the injury-feigning 'broken-wing' display.
Approach	Parent bobwhite approached observers during behavioral observations. Approaches either happened while performing distraction displays or by simply running at observers.

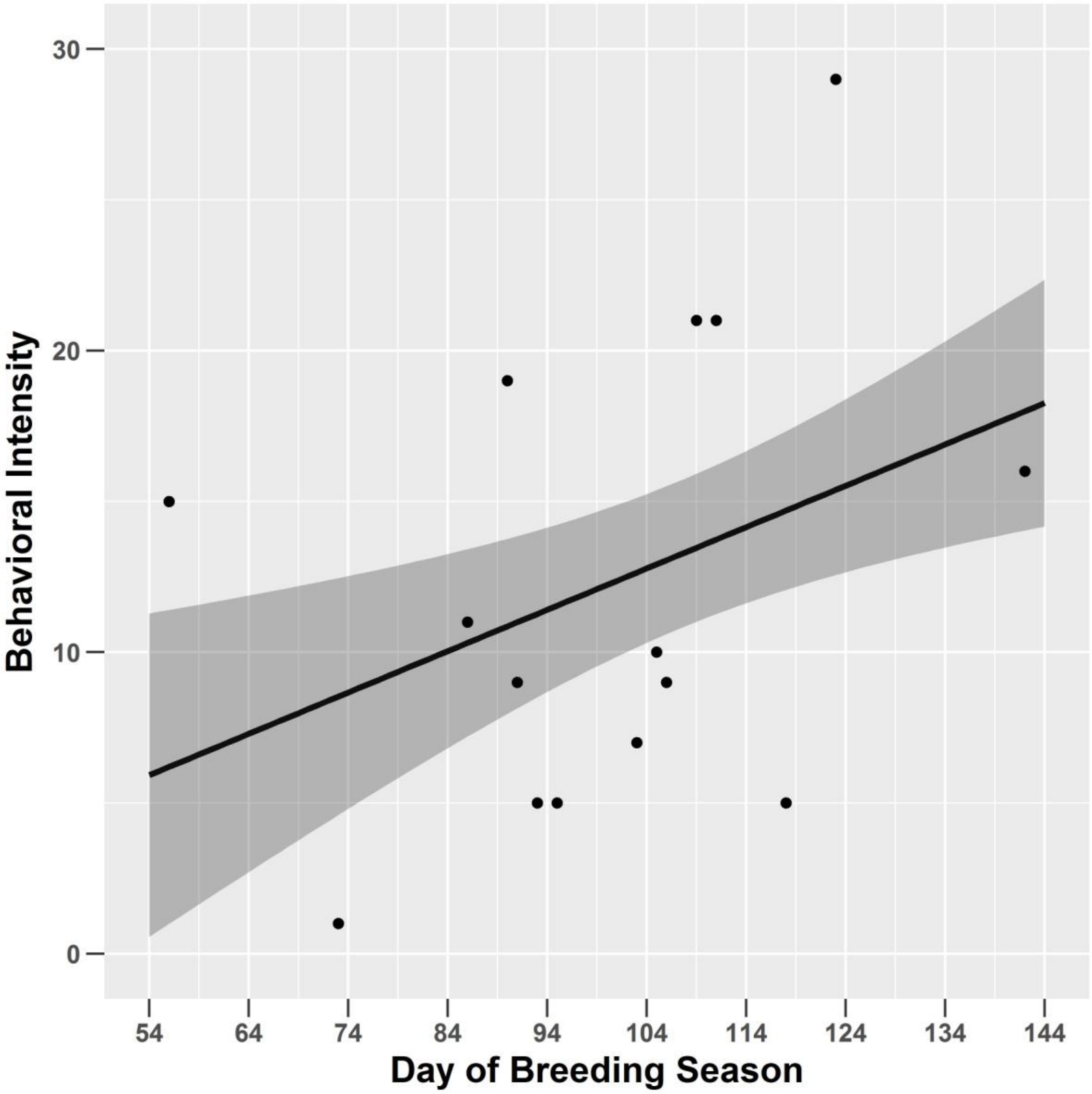
Variable	**Beta Estimates**	**Standard Error**	**T-Value**	**P-Value**
Intercept	12.73	4.10	3.11	0.01
Day.Number	4.88	2.24	2.18	0.05
BroodSize	1.80	2.41	0.75	0.47
Mass	1.90	2.87	0.66	0.52
GroupTR	1.59	5.26	0.30	0.77
AgeAdult	–1.22	4.00	-0.31	0.77

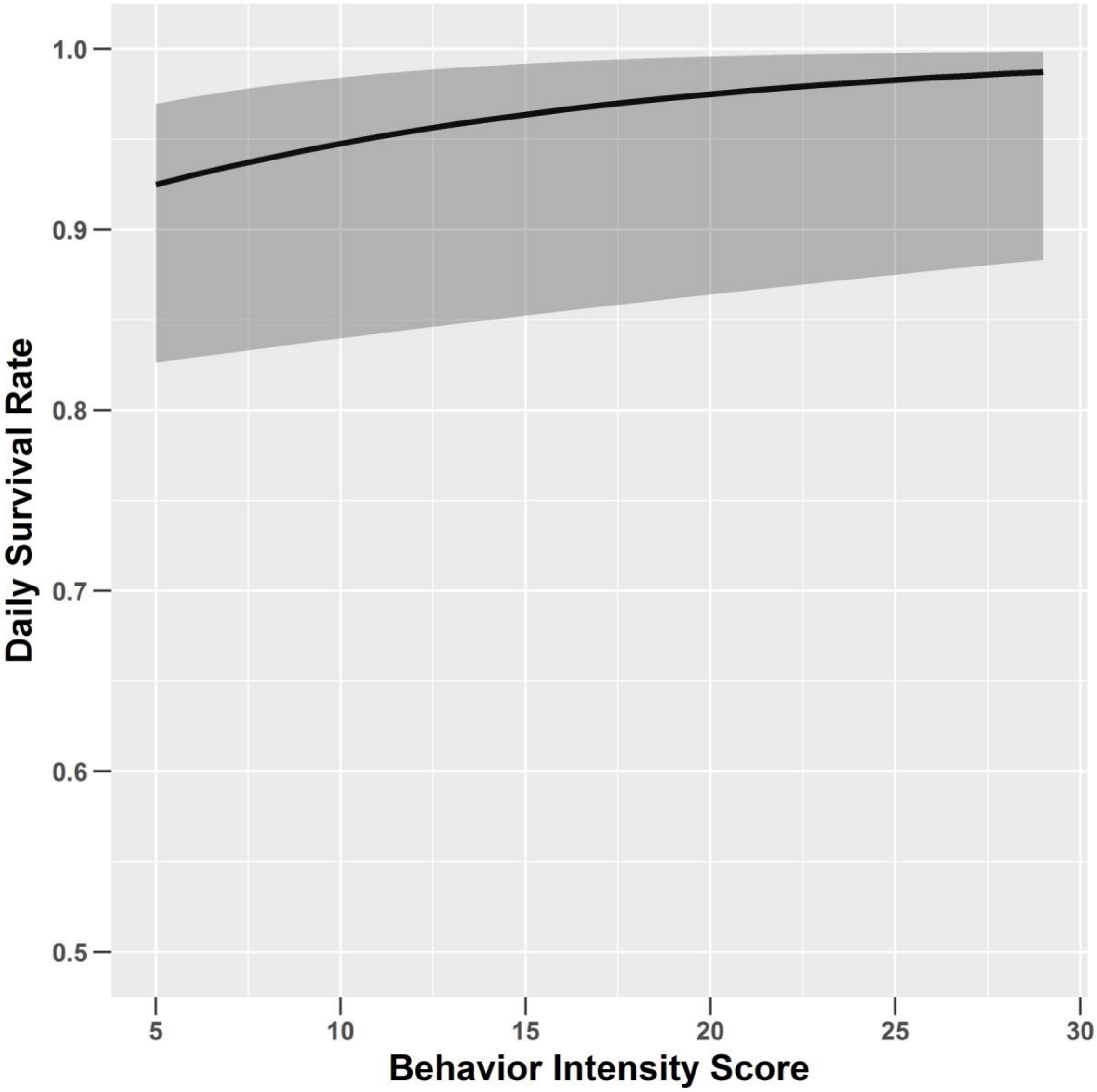
Model	AICc	ΔAICc	w_i	k	Deviance
Temporal Variation					
Null	123.71	0	0.53	1	76.19
Year[a]	125.69	1.97	0.19	2	76.13
HatchDay	125.69	1.98	0.19	2	121.65
Year + HatchDay	127.49	3.77	0.08	3	121.40
Group					
Null	123.71	0	0.73	1	76.19
Status	125.73	2.01	0.27	2	121.69
Age and Morphometrics					
Null	123.71	0	0.22	1	76.19
Mass	124.63	0.91	0.14	2	120.59
Age	124.71	1.00	0.13	2	120.67
Tarsus	125.26	1.54	0.10	2	121.22
LWC	125.57	1.85	0.09	2	121.52
Age + Mass	125.84	2.12	0.07	3	119.75
Age + QAge[a]	126.14	2.42	0.06	3	120.05
Age + Tarsus	126.30	2.59	0.06	3	120.21
Age + LWC	126.71	3.00	0.05	3	120.63
Age + QAge[a] + Mass	127.50	3.78	0.03	4	119.35
Age + Qage[a] + Tarsus	127.68	3.97	0.03	4	119.53
Age + QAge[a] + LWC	128.11	4.39	0.02	4	119.96
Weather Effects					
Precip	118.77	0	0.89	2	114.72
Null	123.72	4.94	0.08	1	76.19
Sig. Rain Days	125.70	6.92	0.03	2	121.65
Behavior Covariates					
Precip + Intensity	116.61	0.00	0.33	3	110.52
Precip + Parent + Intensity	118.12	1.51	0.16	4	109.97
Precip + Intensity + QIntensity	118.21	1.61	0.15	4	110.06
Precip	118.77	2.16	0.11	2	114.73
Precip + Parent	119.19	2.58	0.09	3	113.10
Precip + Parent + Intensity + QIntensity	119.63	3.02	0.07	5	109.40
Precip + Parent*Intensity	120.19	3.58	0.06	5	109.96
Precip + Parent * Intensity + QIntensity	121.12	4.51	0.03	6	108.80

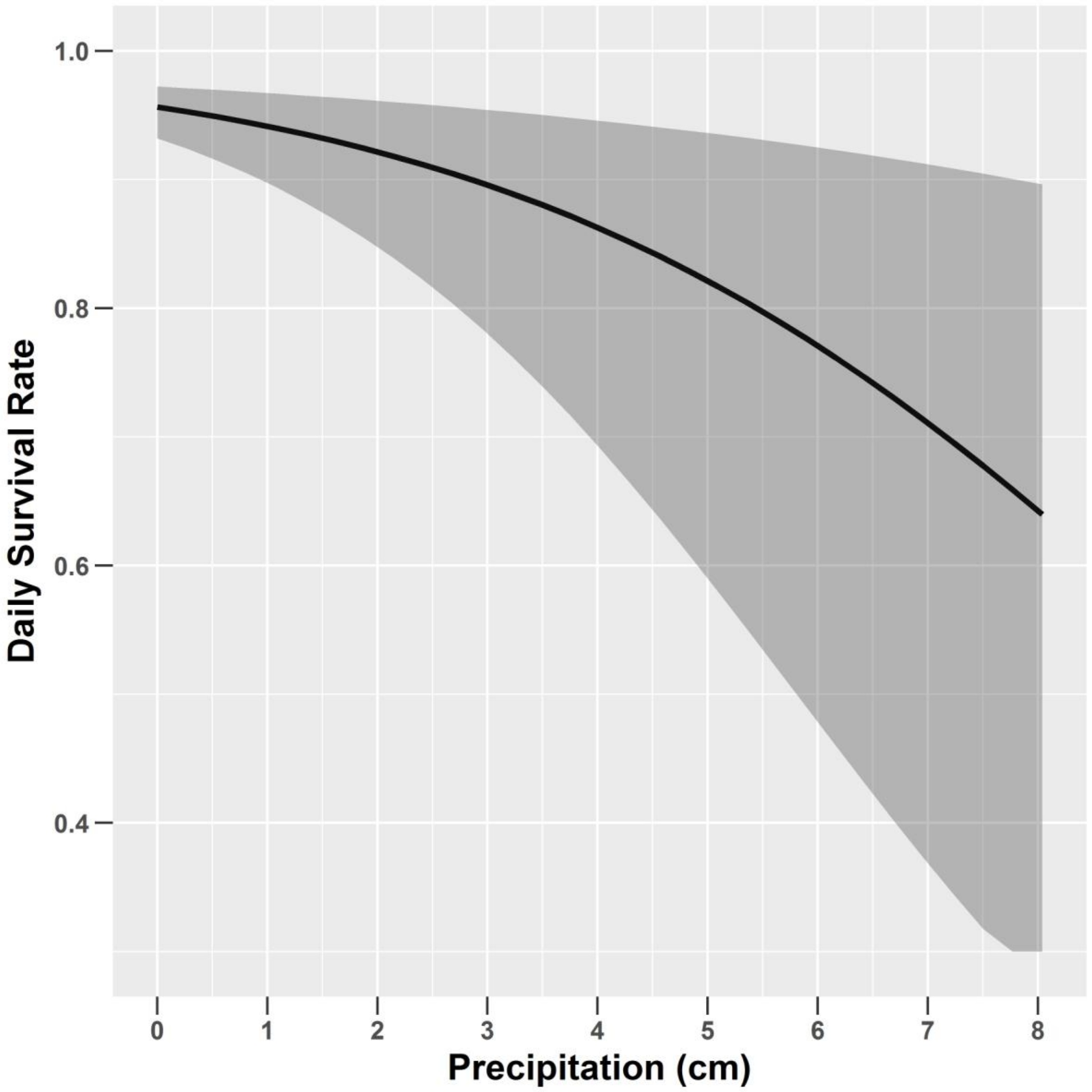
[a] Models with interactions contain main effects


L..Flight
FlyAway
Approach
Run
MultAd
Hold
Res
TR
L.FlightBW
Escape
NMDS2
0.5
0.0
-0.5
-1
0
1
2
NMDS1


MultAd
RunBW
Approach
Run
Escape
NMDS1
NMDS2
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
-1.0
-0.5
0.0
0.5
1.0


30
20
10
0
Behavioral Intensity
54
64
74
84
94
104
114
124
134
144
Day of Breeding Season


1.0
0.9
0.8
0.7
0.6
0.5
Daily Survival Rate
5
10
15
20
25
30
Behavior Intensity Score


Daily Survival Rate
1.0
0.8
0.6
0.4
0
1
2
3
4
5
6
7
8
Precipitation (cm)

CHAPTER 4

Summary and Concluding Remarks

Northern bobwhite populations have been experiencing precipitous population declines since the 1960s (Brennan 1991, Hernández et al. 2013). Habitat management efforts by state agencies, federal agencies, and non-profit organizations (e.g. Conservation Reserve Program, Bobwhite Quail Initiative) encouraged land managers and owners to implement habitat management practices however, range wide declines still remain (Sauer et al. 2013). These declines warrant the need to continue more aggressive restoration techniques like translocation to elicit population responses following habitat restoration. Currently, bobwhite reintroductions are still in their infancy and more work is needed to estimate population parameters post-translocation. These estimates are needed so the efficacy of translocation to establish and sustain viable bobwhite populations can be fully evaluated using rigorous experimental design and properly planned post-release monitoring (Armstrong and Seddon 2008). Previous studies have estimated adult survival, home range/movements, and select reproductive metrics (nests per hen, etc.) post-translocation to provide information on how well reintroduced bobwhites are able to survive and breed in novel landscapes (Kabat and Thompson 1963, Terhune et al. 2006b, a, 2010, Scott et al. 2013, Wiley et al. 2017). However, no studies have estimated direct survival estimates of bobwhite chicks post-translocation to determine if translocated bobwhites are able to successfully raise offspring to independence. We were able to radio-tag 110 individual bobwhite chicks during this project and address an important need in the bobwhite and reintroduction literature.

Our period survival estimates for radio-tagged resident and translocated bobwhite chicks were 27% (2016) and 10% (2017), which lower than current published survival estimates of radio-tagged bobwhite chicks ranging from 36.7–52% (DeMaso et al. 1997, Suchy and Munkel 2000, Lusk et al. 2005). These estimates mean bobwhites may experience lower offspring survival rates following translocation, which may carry implications for short-term population responses following release. Although managers should consider multiple life history characteristics (adult survival, etc.) and how they contribute to species population growth (Stahl and Oli 2006), low offspring survival rates may need to be offset by increasing the number of bobwhites released so that population growth can occur. These initial breeding efforts are imperative for reintroduction success in short-lived species such as the bobwhite where annual survival rates are typically low and future reproductive opportunities are limited (Roseberry and Klimstra 1984, Burger et al. 1995a, DeMaso et al. 1997, Terhune et al. 2007).

Survival rates for resident and translocated offspring did not differ in our study, indicating habitat restoration and management provided the necessary resources for translocated bobwhites to raise offspring successfully and integrate into the current population. These results suggest that bobwhites can be translocated between landscapes (our study, old field succession to longleaf-pine savanna) without detrimental effects on offspring production. Offspring growth rates were lower for translocated bobwhites indicating there may be some differences in the abilities of translocated bobwhites to locate high quality brood-rearing areas possibly due to timing of translocation just prior to the breeding season. Lack of landscape knowledge may limit foraging efficiency of bobwhite chicks in novel environments (Yoder et al. 2004). Although offspring growth rates were lower for translocated bobwhites, these did not result in reduced fitness indicating translocation effects on chick physiology may be temporary. Additional information on bobwhite chick growth post-translocation may still be needed to assess how habitat restoration provides important food and cover resources and how bobwhites are able to locate resources conducive to chick growth and survival. Growth rates may impact time-to-fledging in bobwhite chicks which would require increased parental investment from brooding adults and limit opportunities for multiple nesting attempts (Klimstra and Roseberry 1975, Burger et al. 1995b, Gebhardt-Henrich and Richner 1998).

We also wanted to determine if translocation impacted innate behavioral patterns in northern bobwhites, specifically parental investment (brood defense behaviors) strategies. Disparities in release and donor sites conditions (e.g. predator communities) could make certain innate offspring defense behaviors maladapted if predator communities differ between release and donor sites. These differences could impact adult and offspring survival rates during the breeding season. We found that offspring defense behaviors did not differ between translocated and resident bobwhites which could portend that these behaviors have been selected through many generations and a multitude of predator interactions (Davies et al. 2012). Predator communities may vary by species, but not differ in their function (i.e. foraging strategies and times) which could explain the ability of defense behaviors to be effective against multiple species (Sih et al. 1998). We found that intensive brood defense behaviors did positively impact chick survival in a subset of our study population. Intensive brood defense behaviors may be important in mitigating mortality losses in vulnerable offspring where snakes (*Coluber constrictor, Pantherophis guttatus, amd Agikistrodon piscivorous*) and mammals (ground predators) are primary sources of mortality. Additionally, if behaviors that have been selected for through multiple generations are suppressed or maladapted to local predator communities then adult and offspring survival rates may be negatively affected thus increasing the chance of reintroduction failure.

Future Research

Bobwhite translocation and reintroductions offer a wealth of opportunities to test hypotheses apposite to reintroduction success. Simple modifications to the translocation process offer opportunities to test hypotheses about how timing of release may impact survival rates of adults and offspring. Earlier release periods may allow adults to locate higher quality breeding locales, which may be reflected in offspring performance and survival during the year of release. Changes in spatial distribution of release sites, release group sizes, and optimal sex ratios of release groups may be worthy of future research. These factors may help determine optimal release strategies in relation to how individuals selected for release and release process may impact project success. Population sources could also be compared to determine if localized adaptation improves chances of translocation success with regards to survival (adult and chick) and reproduction.

Continued research may be needed to determine how growth rates are impacted by translocation. We compared offspring growth rates of translocated and resident chicks, however, additional comparisons could be made between chicks at release sites and donor sites to determine if offspring of translocated bobwhites perform at similar levels to those in their native habitat. Diet studies may also be useful to determine if translocated individuals are able to adapt to potential disparities in natural food availability between release and donor sites. Daily movements and home ranges also offer future avenues of research in translocated bobwhites. If translocated bobwhites need to move more often to locate important food and cover resources then this may carry implications for adult and chick survival (Yoder et al. 2004) in novel landscapes thus limiting reintroduction success. Availability of alternative prey species and estimation of key predator populations pre- and post-translocation can also give resource managers an idea about probability of project success and predator response to introduction of a new prey base.

Our project represents only one translocation of bobwhites without spatial replication (i.e. one release site) and lacks a true control. However, the establishment of successful breeding at our study site offers hope that translocation into managed landscapes can expedite population recovery following habitat restoration. We recommend that our experiment be replicated to determine how bobwhites are affected by translocation, however, site evaluations should occur prior to translocation to identify important habitat characteristics and other obstacles to reintroduction success. These site evaluations are imperative so that testable hypotheses can be formed, experiments designed, and monitoring plans executed to determine factors that limit and/or promote restoration success.

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