BioOne COMPLETE

Environmental and behavioral factors affect northern bobwhite offspring survival

Authors: Lunsford, Kyle D., Roberts, Thomas B., Terhune, Theron M., and Martin, James A.

Source: Wildlife Biology, 2020(3)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00630

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Wildlife Biology 2020: wlb.00630
doi: 10.2981/wlb.00630
© 2020 The Authors. This is an Open Access article
Subject Editor: Yuehua Sun. Editor-in-Chief: Ilse Storch. Accepted 3 July 2020

Environmental and behavioral factors affect northern bobwhite offspring survival

Kyle D. Lunsford, Thomas B. Roberts, Theron M. Terhune and James A. Martin

K. D. Lunsford, T. B. Roberts and J. A. Martin ✉ (jmart22@uga.edu), Univ. of Georgia, 180 E. Green Street, Athens, GA 30602, USA. – T. M. Terhune, Tall Timbers Research Station and Land Conservancy, Tallahassee, FL, USA.

Many environmental and behavioral factors can affect offspring survival, and these factors can vary by species. Parental investments, defense or distraction displays, and translocation can potentially affect survival of young. Alterations in parental investment strategies may carry implications for population growth due to lower offspring survival in translocated bobwhites. We hypothesized that translocation would not impact brood defense behaviors in bobwhites as predator communities may be similar between donor sites (Florida) and release sites (North Carolina). However, we hypothesized that brood defense behaviors affect offspring survival rates. We conducted defense behavior observations by approaching brood-rearing bobwhites and recording exhibited behaviors, and assigned scores based on behavioral intensity. We used the corral capture method and modified-suture technique to capture and radio-tag bobwhite chicks. Brood defense behaviors did not differ between resident and translocated bobwhites. We observed seven different brood defense behaviors: fly away, run, labored flight, labored flight with broken wing display, run with broken wing display, hold tight and approach behaviors. We found that time-varying precipitation and behavioral intensity affected bobwhite chick survival. These results indicate that translocation does not impact brood defense behaviors due to behavioral similarities between resident and translocated cohorts. These results portend that some variation in annual chick mortality cannot be mitigated by habitat management. We also provide evidence that translocation does not alter/suppress important behavioral patterns in bobwhite, indicating it is a viable method for restoring bobwhite populations in conjunction with habitat management.

Keywords: brood defense, *Colinus virginianus*, northern bobwhite, offspring survival, parental investment, predation

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). Parental investment strategies vary across species whereas tradeoff 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). In northern bobwhites *Colinus virginianus*, parental investment behaviors include finding mates, nest building, egg production, incubation, brooding (offspring thermoregulation), anti-predator 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 behaviors 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

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <http://creativecommons.org/licenses/by/4.0/>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

offspring. As such, the tradeoffs between investing in current offspring, future offspring and parent survival 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. 1995b) 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/parent survival) to intense displays (investment in current offspring). Reproductive cost may outweigh perceived predation risk inciting instantaneous parental behaviors regarding protection of offspring during predator encounters (Dawkins and Carlisle 1976, Smith 1977, Andersson et al. 1980). Early nest failure(s) coupled with limited time to successfully reproduce may elicit riskier behaviors such as defending young. In contrast, long breeding seasons (Klimstra and Roseberry 1975, Roseberry and Klimstra 1984, Burger et al. 1995b) individuals may not defend current offspring early in the season to defer investment to future offspring (within the same season). However, high mortality rates (Burger et al. 1995a, 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 behaviors on fitness may be exacerbated by translocation 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 differs 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 adversely affect parental investment behaviors of translocated birds, resulting in offspring survival consequences.

In addition to the effects of behavior, environmental factors can affect survival of precocial young (Erikstad and Andersen 1983). For example, Terhune et al. (2019) found that rainfall had a negative effect on bobwhite chick survival. Rainfall could affect foraging leading to reduced growth limiting their ability to escape predators (Erikstad and Spidsø 1982, Erikstad and Andersen 1983). It could also improve their detection by predators by amplifying scent or increasing predator movements. Moreover, it could have direct effects on survival through hypothermia as rainfall is often associated with cooler temperatures (Korschgen et al 1996). Furthermore, we included the influence of rainfall in our models as we expected it to possibly mediate the influence of parental behaviors – the latter being the main focus of this study.

Despite bobwhites being one of 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. Knowing the similarities in the behaviors and subsequent survival of offspring will inform future bobwhite populations. If the behaviors and survival were found to be different, the source of translocated birds would be in question. However, in this case we expected that translocation would 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.

Material and methods

Study area

Our study occurred on a private property in Brunswick County, North Carolina, USA. The study site was located in the Carolina flatwoods ecoregion (Griffith et al. 2002). Temperature ranges for Brunswick County, NC are 18–34°C in June through September (National Climate Data Center, National Oceanic and Atmosphere Administration). Average daily rainfall during the breeding season on our study site was 0.63 cm (0–20.4 cm) per day in 2016, and 0.50 cm (0–5.54 cm) per day in 2017 (National Climate Data Center, National Oceanic and Atmospheric Administration). Our study site was 2586 ha and contained 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 *P. taeda* and live oak *Quercus virginiana* that were thinned to a basal area of 1.2–2.4 $m^2 ha^{-1}$ a 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. Management prescriptions of source sites include maintenance of low basal area upland pine forests (e.g. 3–9 $m^2 ha^{-1}$) dominated by shortleaf *P. echinata* and loblolly 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* spp., forbs

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Solidago spp., *Chamaecrista fasciculata*, *Ambrosia artemisifolia* and blackberry *Rubus* spp. Hardwood hammocks/drains and annually disked fallow fields were also interspersed throughout the landscape (Staller et al. 2005, Ellis-Felege et al. 2012, Jackson et al. 2018).

Capture

We captured resident bobwhites during spring (March) and winter (December) trapping periods, 2016–2017, 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 (≥ 132 g) after collecting morphometric (e.g. wing chord length, tarsus length and mass). Trapping methodologies were identical for donor and source sites.

Translocation of bobwhites occurred annually ($n_{2016} = 266$, $n_{2017} = 270$) over the two-year study from three properties in Red Hills region of northern Florida. Two of our source sites were 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), and 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 m on either side of estimated location. Nest sites were checked daily from about 25 m away 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 et al. (2019). 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). Briefly, we located the roosting brood several hours before sunrise and then constructed a corral around the roosted brood. 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 using radio-telemetry, however, FLIR E-Series forward-looking infrared cameras (hereafter, FLIR) (FLIR Systems, Wilsonville, OR, USA) 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. At sunrise vegetation was removed by hand within the corral to more easily capture chicks.

We used a 30 g spring scale 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 days) 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. 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 (Terhune et al. 2020).

Brood defense

We conducted brood defense encounters when chicks of each brooding bobwhite were 2–4 days old. Broods were only approached once to minimize any impacts on survival. 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 h 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 (10 m). 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.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 1. Brood defense behaviors exhibited by northern bobwhites *Colinus virginianus* during simulated predator encounters conducted on a private property in Brunswick County, NC, USA 2016–2017. The score value indicates the subjective value each behavior was given to indicate the amount of parental investment (larger values = greater investment).

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

Brooding adults were pursued about 10 m from encounter locations 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. The same observer collected all of the information. 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 (Table 1). We summed defense behavior values to create a cumulative score based on all exhibited behaviors of all brood-rearing bobwhites. For example, an adult that made an aggressive 'approach' to the observer received a score of 7. If that bird also ran with a broken wing (a score of 6) the cumulative score would have been 13. Multiple adults exhibiting behaviors increased scores for the respective behaviors displayed for each adult and then summed. For example, two adults running with a broken wing would result in a score of 12.

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 (<www.r-project.org>) 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 fit linear models to ordination scores ($\alpha = 0.15$) of resident and translocated bobwhites to determine if brood-rearing strategies were differed among the two groups, and 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. Chicks were tracked daily during this period of time. 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 et al. 2019, Terhune et al. 2019). Morphometric measurements (mass, left wing chord and tarsus) were included as continuous variables in our survival analysis to serve as a proxy for growth. 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, Southport, NC; about 17 km from study area). Our daily precipitation

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

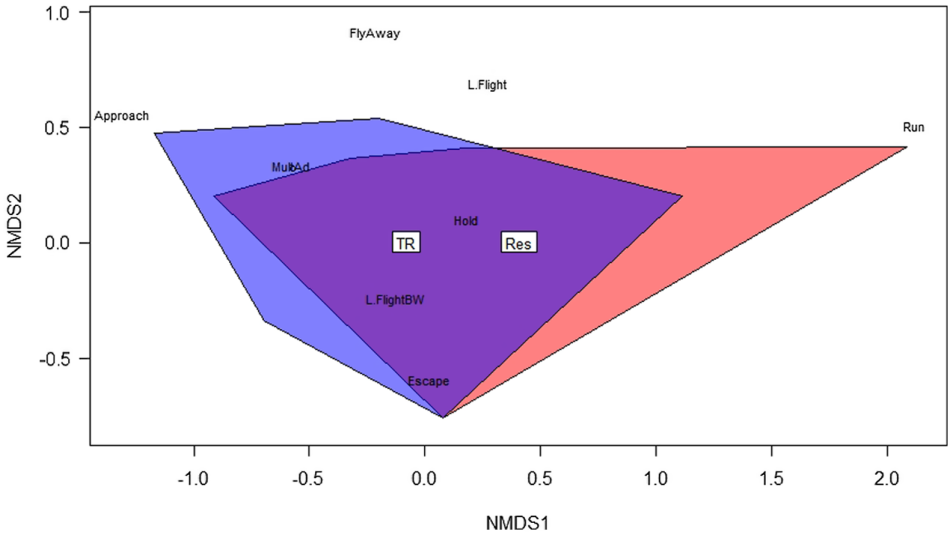


Figure 1. Graphical ordination (non-metric multidimensional scaling) of defense behaviors of resident (n = 7) and translocated (n = 10) northern bobwhites *Colinus virginianus* during simulated predator encounters conducted on a private property in Brunswick County, NC, USA, 2016–2017.

data was taken from June to October, 2016–2017. We used daily precipitation values as time-varying covariates in our survival analysis. 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 but 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 small sample corrected Akaike's information criterion (AIC_c); models with the lowest AIC_c values were considered to be best approximating models in each model step (Burnham and Anderson 1998). We evaluated model similarity using ΔAIC_c values; values that were ≤ 4 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

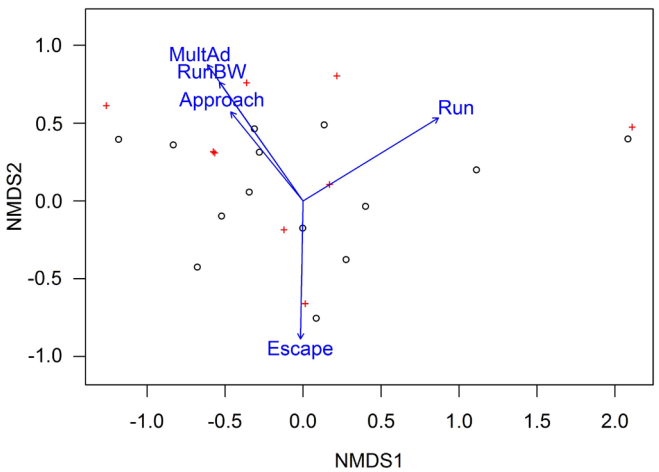


Figure 2. Graphical ordination (non-metric multidimensional scaling) of defense behaviors of all northern bobwhites *Colinus virginianus* during simulated predator encounters (n = 17) conducted on a private property in Brunswick County, NC, US, 2016–2017.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

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 property in Brunswick County, NC, USA 2016–2017.

Variable	Beta estimates	SE	T-value	p-value
Intercept	12.73	4.10	3.11	0.01
Day number	4.88	2.24	2.18	0.05
Brood size	1.80	2.41	0.75	0.47
Mass	1.90	2.87	0.66	0.52
Group-translocated	1.59	5.26	0.30	0.77
Age-adult	−1.22	4.00	−0.31	0.77

model to facilitate interpretation of effect sizes and comparison among predictor variables (Arnold 2010).

Results

We conducted brood defense encounters on 17 bobwhite broods ($n_{Resident} = 6$, $n_{Translocated} = 11$, $n_{adult} = 6$, $n_{juvenile} = 11$, $n_{2016} = 7$, $n_{2017} = 10$) and radio-tagged 73 individual bobwhite chicks ($n_{Resident} = 25$, $n_{Translocated} = 48$, $n_{2016} = 25$, $n_{2017} = 48$) in 2016–2017. Initially 20 broods were tagged but 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 ($\dot{x}$ - NMDS 1: −0.083, NMDS 2: −0.068) and resident bobwhites ($\dot{x}$ - NMDS 1: 0.119, NMDS 2: 0.098) based on ordination of defense behaviors (Fig. 1) and linear models (NMDS 1: $p = 0.605$, $df = 1$, NMDS 2: $p = 0.437$, $df = 1$). Our behavioral observations yielded seven 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),

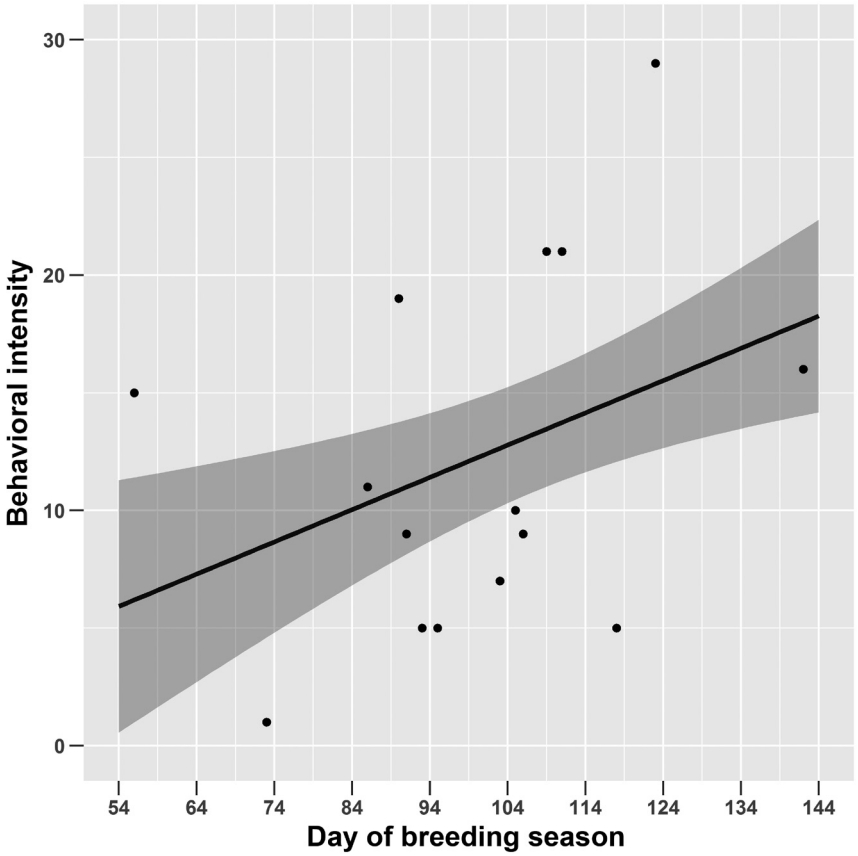


Figure 3. Model predicted (solid black line) and raw behavioral intensity scores (points) of brood-rearing northern bobwhites *Colinus virginianus* and 85% confidence limits (shaded area) across day of breeding season on a private property in Brunswick County, NC, USA, 2016–2017.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

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.

Model	AIC_c	ΔAIC_c	w_i	k	Deviance
Temporal variation					
Null	123.71	0	0.53	1	76.19
Year	125.69	1.97	0.19	2	76.13
Hatch day	125.69	1.98	0.19	2	121.65
Year + Hatch day	127.49	3.77	0.08	3	121.40
Group					
Null	123.71	0	0.73	1	76.19
Translocation 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
Left wing chord	125.57	1.85	0.09	2	121.52
Age + Mass	125.84	2.12	0.07	3	119.75
Age + Quadratic age	126.14	2.42	0.06	3	120.05
Age + Tarsus	126.30	2.59	0.06	3	120.21
Age + Left wing chord	126.71	3.00	0.05	3	120.63
Age + Age^2 + Mass	127.50	3.78	0.03	4	119.35
Age + Age^2 + Tarsus	127.68	3.97	0.03	4	119.53
Age + Age^2 + Left wing chord	128.11	4.39	0.02	4	119.96
Weather effects					
Daily precip.	118.77	0	0.89	2	114.72
Null	123.72	4.94	0.08	1	76.19
Behavior covariates					
Daily precip. + Intensity	116.61	0.00	0.33	3	110.52
Daily precip. + Parent + Intensity	118.12	1.51	0.16	4	109.97
Daily precip. + Intensity + $Intensity^2$	118.21	1.61	0.15	4	110.06
Daily precip.	118.77	2.16	0.11	2	114.73
Daily precip. + Parent	119.19	2.58	0.09	3	113.10
Daily precip. + Parent + Intensity + $Intensity^2$	119.63	3.02	0.07	5	109.40
Daily precip. + Parent × Intensity	120.19	3.58	0.06	5	109.96
Daily precip. + Parent × Intensity + $Intensity^2$	121.12	4.51	0.03	6	108.80

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 decisions (long distance flight away from brood during encounter). We found six brood defense characteristics that predicted ordination of defense strategies of brood-rearing bobwhites (Fig. 2); 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 (Table 2, Fig. 3; $\beta_{Day.Number}$ = 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 3) indicating there were no significant time trends in bobwhite chick survival over the study period. Other candidate hypotheses in this model step were competitive ($\leq 4\ \Delta AIC_c$), 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 defense behavior intensity improved model fit. Defense behavior intensity impacted chick survival. Our most parsimonious model ($\beta_0 + \beta_{Precip} + \beta_{Intensity}$) included defense behavior intensity (Fig. 4; $\beta_{Intensity}$ = 0.58, 85% CI = 0.27–0.89) and effects time-varying precipitation (Fig. 5; β_{Precip} = −0.31, 85% CI = −0.36 to −0.14).

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 in survival analyses. Our neutral prediction regarding differences in parental investment strategies between resident and translocated bob-

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

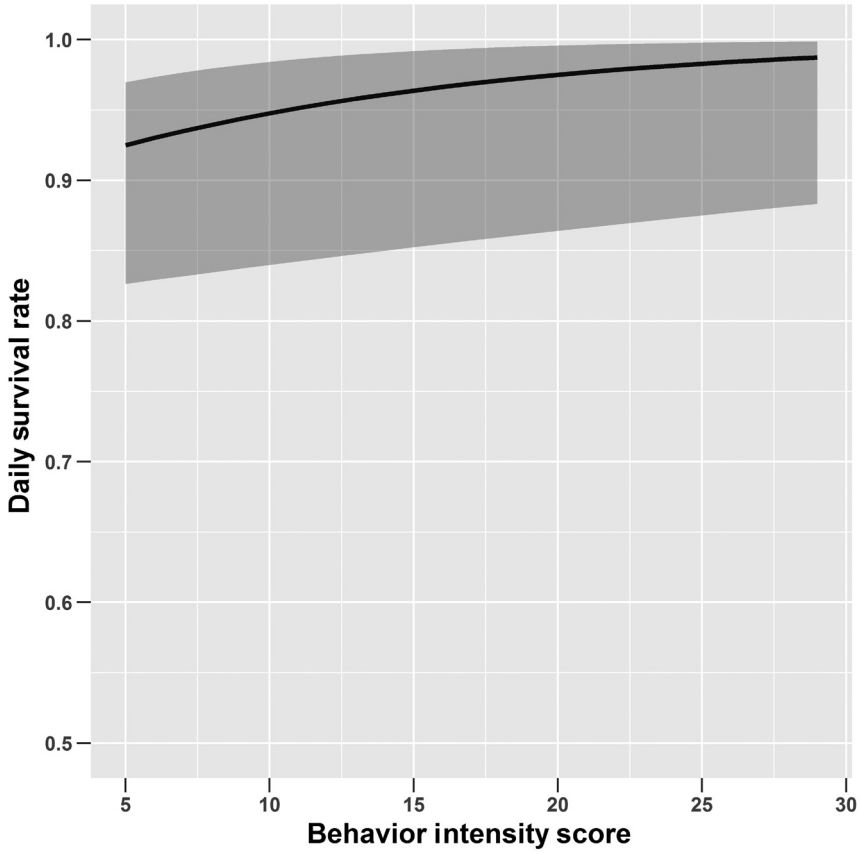


Figure 4. Top model predicted daily survival rate (DSR) of radio-tagged northern bobwhite chicks (solid black line) and 85% confidence limits (shaded area) across scored defense behaviors of brood-rearing northern bobwhites *Colinus virginianus* on a private property in Brunswick County, NC, USA, 2016–2017.

whites 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 similar brood defense behaviors as other game birds. Red grouse *Lagopus lagopus scoticus*, black grouse *Tetrao tetrix* and western capercaillie *T. 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. We observed low rates of 'no defense' or outright fleeing behavior in brooding adults. Broods represent a successful breeding attempt that 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 release 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 instan-

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

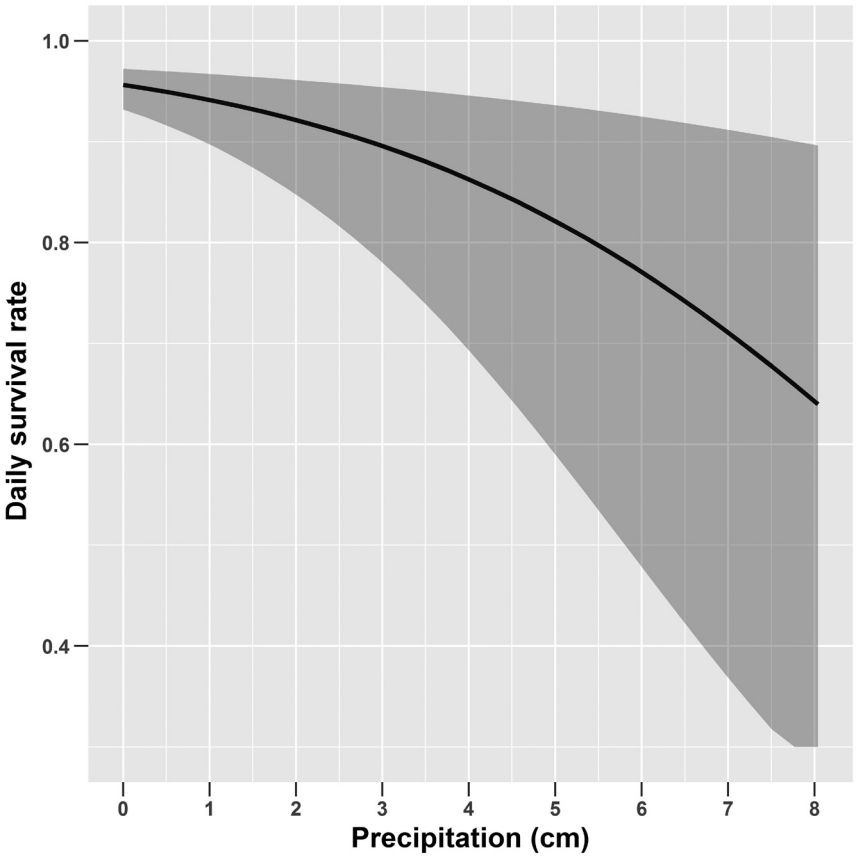


Figure 5. Top model predicted daily survival rate (DSR) of radio-tagged northern bobwhite *Colinus virginianus* chicks (solid black line) and 85% confidence limits (shaded area) across precipitation (cm) values on a private property in Brunswick County, NC, USA, 2016–2017.

taneous decisions regarding the defense of offspring, while maximizing their own survival (Veen et al. 2000, Staller et al. 2005, Ellis-Felege et al. 2013).

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 patterns in brood defense behaviors among brood-rearing bobwhites considering species-specific 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).

Congruent with other literature on bobwhites we found that rainfall negatively affected survival of bobwhite chicks (Terhune et al. 2019). However, the results herein do conflict somewhat with a Lunsford et al. (2019) that was conducted in parallel to this paper. The Lunsford et al. (2019) paper did not find support the influence of rainfall on chick survival. However, the Lunsford et al. (2019) analysis was done over a longer survival period (> 90 days post hatch versus 21 days post hatch in this paper) that may have obscured the effects of rainfall that occurred in the first few weeks of life, that is, other variables affect survival later in the development period. Also, the importance of parental behavior was precluded from Lunsford et al. (2019) because not all broods in that study were sampled as they were in this study not allowing the inclusion of parental behaviors. There may be a confounding or an interacting influence of rainfall and parental care that needs future study. Nonetheless, rainfall likely plays a direct role in survival of chicks as shown in other species (Gregg et al. 2007). Terhune et al. (2019) found that rainfall during the first 28 days since hatch had a negative influence on survival. Similar results have been found with other Galliformes throughout the world (Erikstad and Spidsø 1982, Erikstad and Andersen 1983). We used a time-varying covariate and a linear effect of rainfall. Future studies should consider non-linear and threshold effects of rainfall and interactions with temperature in their survival models.

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

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

season. In addition, we only observed defense behaviors 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 once during brooding. We may have not captured the predominant behavior by an adult but we likely captured the predominate behaviors between the resident and translocated birds. Additionally, subjective scoring of defense behavior intensity may not accurately reflect true risk/intensity of behaviors. Lastly, our sample sizes were modest necessitating replication in future studies. 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 ongoing evaluation of translocation as a population restoration method needs to continue discovering factors that may limit the success of translocation. Our research suggests that translocation does not suppress innate behaviors or alter parental investment strategies of bobwhites that are conducive to offspring survival.

Acknowledgements – We owe a great debt of gratitude to Belvedere Property Management, LLC for funding our research and providing a study site to further the cause of bobwhite conservation. We greatly appreciate the logistical support, financial resources and advice provided by all property managers and staff over the duration of our research. We also thank Tall Timbers Research Station, Dixie Plantation and other properties for assisting in bobwhite translocation. Additionally, we would like to thank all the graduate students and interns (B. Roberts, J. Bishop, Z. Bell, J. Hill) who contributed and assisted with this research. We'd like to thank James Beasley and Mike Conroy for intellectual and statistical guidance.

Author contributions – All authors contributed to this manuscript. The second and third authors provided stylistic and intellectual guidance as well as assistance with data analysis.

Conflicts of interest – There are no conflicts of interest with all affiliated individuals.

Permits – Trapping, handling and tagging procedures were approved by the Florida Fish and Wildlife Commission (Northern Bobwhite Trapping Permit no. 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 Fish and Wildlife Commission (Translocation Permit no. QT-16-01) and the North Carolina Wildlife Resources Commission (17-CSP00501).

References

Anderson, D. R. et al. 2000. Null hypothesis testing: problems, prevalence and an alternative. – J. Wildl. Manage. 64: 912–923.

Andersson, M. et al. 1980. Parental defence of offspring: a model and an example. – Anim. Behav. 28: 536–542.

Armstrong, E. A. 1954. The ecology of distraction display. – Br. J. Anim. Behav. 2: 121–135.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. – J. Wildl. Manage. 74: 1175–1178.

Blancher, P. J. and Robertson, R. J. 1982. Kingbird aggression: does it deter predation? – Anim. Behav. 30: 929–930.

Borchelt, P. and Ringer, R. K. 1973. Temperature regulation development in bobwhite quail (*Colinus virginianus*). – Poult. Sci. 52: 793–798.

Burger, L. W. et al. 1995a. Survival and cause-specific mortality of northern bobwhite in Missouri. – J. Wildl. Manage. 59: 401–410.

Burger, L. et al. 1995b. Reproductive strategies, success and mating systems of northern bobwhite in Missouri. – J. Wildl. Manage. 59: 417–426.

Burkepile, N. A. et al. 2002. Attachment of radio-transmitters to one-day-old sage grouse chicks. – Wildl. Soc. Bull. 30: 93–96.

Burnham, K. P. and Anderson, D. R. 1998. Model selection and multimodel inference: a practical information–theoretic approach. – Springer.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information–theoretic approach. – Springer.

Conkling, T. J. et al. 2015. Assessment of variation of nest survival for grassland birds due to method of nest discovery. – Bird Study 62: 223–231.

Cox, S. et al. 2004. Survival and cause-specific mortality of northern bobwhites in western Oklahoma. – J. Wildl. Manage. 68: 663–671.

Curtis, P. D. et al. 1993. Potential polygamous breeding behavior in northern bobwhite. – Proc. Natl. Quail Symp. 3: 55–63.

Davies, N. B. et al. 2012. An introduction to behavioural ecology. – Wiley-Blackwell.

Dawkins, R. and Carlisle, T. R. 1976. Parental investment, mate desertion and a fallacy. – Nature 262: 131–133.

Dinsmore, S. J. et al. 2002. Advanced techniques for modeling avian nest survival. – Ecology 83: 3476–3488.

Ellis-Felege, S. N. et al. 2012. Predator reduction results in compensatory shifts in losses of avian ground nests. – J. Appl. Ecol. 49: 661–669.

Ellis-Felege, S. N. et al. 2013. Fight or flight – parental decisions about predators at nests of northern bobwhites (*Colinus virginianus*). – Auk 130: 637–644.

Erikstad, K. E. and Spidsø, T. K. 1982. The influence of weather on food intake, insect prey selection and feeding behaviour in willow grouse chicks in northern Norway. – Ornis Scand. (Scand. J. Ornithol.) 13: 176–182.

Erikstad, K. E. and Andersen, R. 1983. The effect of weather on survival, growth rate and feeding time in different sized willow grouse broods. – Ornis Scand. (Scand. J. Ornithol.) 14: 249–252.

Gangloff, E. J. et al. 2018. Among-individual heterogeneity in maternal behaviour and physiology affects reproductive allocation and offspring life-history traits in the garter snake *Thamnophis elegans*. – Oikos 127: 705–718.

Greig-Smith, P. W. 1980. Parental investment in nest defense by stonechats (*Saxicola torquata*). – Anim. Behav. 28: 604–619.

Gregg, M. A. et al. 2007. Use of implanted radiotransmitters to estimate survival of greater sage grouse chicks. – J. Wildl. Manage. 71: 646–651.

Griffith, G. E. et al. 2002. Ecoregions of North Carolina and South Carolina. – Environ. Prot. Agency, pp. 1–31.

Hamilton, W. D. 1971. Geometry for the selfish herd. – J. Theor. Biol. 31: 295–311.

Hudson, P. J. and Newborn, D. 1990. Brood defence in a precocial species: variations in the distraction displays of red grouse, *Lagopus lagopus scoticus*. – Anim. Behav. 40: 254–261.

Jackson, A. L. et al. 2018. Partial meso-mammal predator removal positively affects northern bobwhite reproduction. – Wildl. Biol. 2018: wlb.00357.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Kaler, R. S. A. et al. 2010. Demography of a reintroduced population of Evermann's rock ptarmigan in the Aleutian Islands. – Wilson J. Ornithol. 122: 1–14.
Kenward, R. E. 2001. Historical and practical perspectives. – In: Marzluff, J. and Millspaugh, J. J. (eds), Radio tracking and animal populations. Academic Press, pp. 3–12.
Klimstra, W. D. and Roseberry, J. L. 1975. Nesting ecology of the bobwhite in southern Illinois. – Wildl. Monogr. 41: 3–37.
Korschgen, C. E. et al. 1996. Survival of radiomarked canvasback ducklings in northwestern Minnesota. – J. Wildl. Manage. 60: 120–132.
Knight, R. L. and Temple, S. A. 1986. Why does intensity of avian nest defense increase during the nesting cycle? – Auk 103: 318–327.
Knight, R. L. and Temple, S. A. 1988. Nest-defense behavior in the red-winged blackbird. – Condor 90: 193–200.
Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. – Psychometrika 29: 115–129.
Laake, J. and Rexstad, E. 2008. Appendix C: RMARK – an alternative approach to building linear models in MARK. – In: Program MARK: a gentle introduction. pp. C1–C111. <www.phidot.org/software/mark/docs/book/pdf/app_3.pdf>.
Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – Can. J. Zool. 68: 619–640.
Lunsford, K. D. et al. 2019. Survival and growth of northern bobwhite offspring post-translocation. – J. Wildl. Manage. 83: 1326–1335.
Martin, K. 1984. Reproductive defence priorities of male willow ptarmigan (*Lagopus lagopus*): enhancing mate survival or extending paternity options? – Behavioral Ecol. Sociobiol. 16: 57–63.
Miller, R. C. 1922. The significance of the gregarious habit. – Ecology 3: 122–126.
Montgomerie, R. D. and Weatherhead, P. J. 1988. Risks and rewards of nest defence by parent birds. – Q. Rev. Biol. 63: 167–187.
Paasivaara, A. and Pöysä, H. 2007. Survival of common goldeneye *Bucephala clangula* ducklings in relation to weather, timing of breeding, brood size and female condition. – J. Avian Biol. 38: 144–152.
Pedersen, H. C. and Steen, J. B. 1985. Parental care and chick production in a fluctuating population of willow ptarmigan. – Ornis Scand. 16: 270–276.
Petrides, G. A. and Nestler, R. B. 1943. Age determination in juvenal bob-white quail. – Am. Midl. Nat. 30: 774–782.
Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. – Oikos 44: 257–267.
Roseberry, J. L. and Klimstra, W. D. 1984. Population ecology of the bobwhite. – Southern Illinois Univ. Press.
Sandercock, B. K. 1994. The effect of manipulated brood size on parental defence in a precocial bird, the willow ptarmigan. – J. Avian Biol. 25: 281–286.
Sih, A. et al. 1998. Emergent impacts of multiple predators on prey. – Trends Ecol. Evol. 13: 350–355.
Smith, J. M. 1977. Parental investment: a prospective analysis. – Anim. Behav. 25: 1–9.
Smith, M. D. et al. 2003. A technique for capturing northern bobwhite chicks. – Wildl. Soc. Bull. 31: 1054–1060.
Sonerud, G. A. 1985. Brood movements in grouse and waders as defense against win-stay search in their predators. – Oikos 44: 287–300.
Sonerud, G. A. 1988. To distract display or not: grouse hens and foxes. – Oikos 51: 233–237.
Spiers, D. E. et al. 1985. Homeothermic development in the bobwhite (*Colinus virginianus*). – Comp. Biochem. Physiol. 81: 921–927.
Staller, E. L. et al. 2005. Identifying predators at northern bobwhite nests. – J. Wildl. Manage. 69: 124–132.
Stoddard, H. L. 1931. The bobwhite quail; its habits, preservation and increase. – Charles Scribner's Sons.
Terhune, T. M. et al. 2007. Factors influencing survival of radiotagged and banded northern bobwhites in Georgia. – J. Wildl. Manage. 71: 1288–1297.
Terhune, T. M. et al. 2010. Translocation to a fragmented landscape: survival, movement and site fidelity of northern bobwhites. – Ecol. Appl. 20: 1040–1052.
Terhune, T. M. et al. 2019. Northern bobwhite chick survival effects of weather. – J. Wildl. Manage. 83: 963–974.
Terhune II, T. M. et al. 2020. A modified suture technique for attaching radiotransmitters to northern bobwhite chicks. – Wildl. Soc. Bull. 44: 396–405.
Trivers, R. L. L. 1972. Parental investment and sexual selection. – In: Sexual selection and the descent of man. Aldine Publishing Company, pp. 136–179.
Trivers, R. L. 1974. Parent–offspring conflict. – Am. Zool. 14: 249–264.
Veen, T. et al. 2000. Experimental evidence for innate predator recognition in the Seychelles warbler. – Proc. R. Soc. B 267: 2253–2258.
Watson, A. and Jenkins, D. 1964. Notes on the behaviour of the red grouse. – Br. Birds 57: 137–170.
White, G. C. and Garrott, R. A. 1990. Analysis of wildlife radio-tracking data. – Academic Press.
Wiklund, C. G. 1990. Offspring protection by merlin *Falco columbarius* females; the importance of brood size and expected offspring survival for defense of young. – Behav. Ecol. Sociobiol. 26: 217–223.
Williams, G. C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. – Am. Nat. 100: 687–690.
Yoder, J. M. et al. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. – Behav. Ecol. 15: 469–476.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use