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FIGHT OR FLIGHT: PARENTAL DECISIONS ABOUT PREDATORS AT NESTS OF NORTHERN BOBWHITES (*COLINUS VIRGINIANUS*)

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ABSTRACT.—Patterns of nest defense against predators by ground-nesting bird species in the wild are poorly understood, largely because of a historical inability to directly monitor nests. Most nest-defense studies have observed responses elicited from artificial predators or human observers presented to nesting birds, and few have attempted to present these events in the context of predator–prey relationships found in the wild. We hypothesized that predator threat level (e.g., the threat posed to the clutch or to the clutch and the attending adult), parental characteristics, clutch investment, and future reproductive opportunities would influence avian nest-defense decisions. During 1999–2006, we examined predation events ($n = 242$) from 790 video-monitored Northern Bobwhite (*Colinus virginianus*) nests. We evaluated parental, predator, daily, and seasonal correlates that potentially contributed to patterns of nest defense by Northern Bobwhites using a model selection approach. The top model showed that nest defense was strongest at nests with larger predators that posed a threat to both adults and the clutch. This model also contained clutch size, but parameter estimates suggest that predator type was the only significant factor determining rates of nest defense. Our results suggest that Northern Bobwhites use the threat posed to the nest and the attending adult by the approaching predator as the primary cue in decisions to engage in nest defense. Received 3 December 2012, accepted 20 September 2013.

Key words: *Colinus virginianus*, nest defense, nest predation, Northern Bobwhite, parental investment, video monitoring.

Lucha o Huída: Decisiones Parentales sobre los Depredadores en los Nidos de *Colinus virginianus*

RESUMEN.—Los patrones de defensa del nido contra depredadores por parte de especies de aves silvestres que anidan en el suelo son pobremente entendidos, en gran parte debido a una inhabilidad histórica para monitorear directamente los nidos. La mayoría de estudios de defensa del nido han observado respuestas desencadenadas por depredadores artificiales o por observadores humanos que se presentan a las aves anidantes, y pocos han intentado presentar dichos eventos en el contexto de las relaciones depredador-presa que se encuentran en condiciones silvestres. Planteamos la hipótesis de que el nivel de amenaza del depredador (e.g. la amenaza impuesta a la nidada o a la nidada y al adulto que cuida de ella), las características de los padres, la inversión en la nidada, y las oportunidades futuras de reproducirse podrían influenciar las decisiones de defensa del nido de las aves. Entre 1999 y 2006 examinamos los eventos de depredación ($n = 242$) de 790 nidos de *Colinus virginianus* monitoreados en vídeo. Evaluamos las variables parentales, del depredador, diarias y estacionales que potencialmente contribuyen a los patrones de defensa del nido por *C. virginianus* usando una aproximación de selección de modelos. El mejor modelo mostró que la defensa del nido fue más fuerte en nidos con depredadores más grandes que amenazaban a la nidada y al adulto que cuidaba de ella. Este modelo también incluyó el tamaño de la nidada, pero los parámetros estimados sugieren que el tipo de depredador fue el único factor que afecta significativamente las tasas de defensa del nido. Nuestros resultados sugieren que *C. virginianus* usa la amenaza impuesta por el depredador que se acerca al nido y al adulto que lo cuida como la pista primaria para la toma de decisiones sobre la defensa del nido.

FIGHT OR FLIGHT? Most birds face this question throughout their lives because predation is a critical factor shaping fitness and, ultimately, decisions related to antipredator behaviors (Ricklefs 1969, Newton 1998, Lind and Cresswell 2005). In particular, nest

predation is the primary cause of nest failure in most bird species (Ricklefs 1969, Martin 1993) and, as a result, birds whose behavioral characteristics facilitate the avoidance or deterrence of nest predation should have higher fitness. “Nest defense” is defined

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as any behavior by the parent that decreases the likelihood of damage to the nest or its contents while simultaneously increasing parental mortality risk (Montgomerie and Weatherhead 1988, Caro 2005). In other words, nest defense is any engagement with a potential predator initiated by the attending parent, and a decision that requires the bird to balance tradeoffs between its own survival and that of its offspring (Trivers 1972).

Many factors can influence whether a bird should stay at a nest and defend its offspring or flee the area in hopes of future reproductive opportunities (Montgomerie and Weatherhead 1988, Caro 2005). Nest defense may increase with the age of the attending bird if probability of mortality varies with age; however, for short-lived species with age-independent mortality, there should be no change in parental risks (Pugesek 1983, Montgomerie and Weatherhead 1988). Nest defense may also be influenced by temporal effects, including the time remaining before a clutch hatches and proximity to the end of the nesting season, because a parent's response may reflect a compromise between investment in a current clutch and survival of the adult to breed in the future (Montgomerie and Weatherhead 1988). Thus, defense should increase as hatching approaches (Biermann and Robertson 1981). Similarly, as the opportunity and probability of re-nesting decrease, one would expect an increase in the value of the clutch and, therefore, a seasonal increase in nest defense (Barash 1975, Ghalambor and Martin 2000). Parental investment theory would predict sex-specific differences in nest defense, yet nest-defense studies vary, with few clear patterns emerging in nature that can be related to theory (for review, see Caro 2005) and many additional factors (re-nesting potential, length of time since egg laying) interacting with sex. Females may be more likely to defend than males because failure of the current clutch would necessitate substantial future investment in laying another clutch, making the current clutch more valuable to her than to the male. In breeding strategies without genetic monogamy, females should defend a nest more rigorously than males because of the increased certainty of parenthood that females have over males (Trivers 1972, Redondo 1989). However, it should be noted that a male may defend more often or intensively if he assumes parental care duties that reduce additional breeding opportunities and if he has paternity of at least some of the clutch (Westneat and Sherman 1993). Finally, larger clutch sizes should reflect a higher potential payoff to birds, and one would thus expect increased defense with increased clutch size if birds are acting optimally (Curio 1987, Caro 2005).

An attending adult's response to a potential predation event at the nest may be predator-specific, varying according to the danger the predator poses to both the nest and the parent (Gochfeld 1984), and may change as the predator approaches the nest (Lima 2009). The perceived danger is likely a direct reflection of the mobility, armament, and size of the predator (Montgomerie and Weatherhead 1988, Caro 2005). Thus, a parent may be more likely to defend against a predator that poses little risk to the parent and less likely to defend against a predator that poses a high risk to both the parent and the nest (Brunton 1990, Dale et al. 1996). Birds, therefore, must be able to identify cues to determine the threat posed by a predator. These cues may be based on predator size in relation to prey size or recognition of armament toward the attending bird that is innate or learned from previous interactions with predators (Caro 2005).

Unfortunately, the role of natural predators in the interaction with birds in the wild has largely gone unstudied (Lima 2002, 2009; Caro 2005) because of logistical constraints in observing such interactions (Ellison and Ribic 2012) or because experimental designs have been simplified to create the consistent predator-prey interaction necessary for evaluating hypotheses related to parental investment theory (Lima 2009). Experimental studies often employ model predators (Curio 1975; Pavel and Bures 2001, 2008) or humans (Barash 1975; Reid and Montgomerie 1985; Weatherhead 1989, 1990; Forbes et al. 1994; Dassow et al. 2012) to elicit nest-defense behavior from birds. Although these experiments have value, particularly for understanding parental investment theory, these approaches limit the value of responses observed, given the dissimilarity to natural predator behaviors typically encountered at nests (Caro 2005).

Nest cameras provide a unique tool for monitoring nesting ecology, identification of predators, and evaluation of avian nest-defense responses to predators in a natural setting (Pietz and Granfors 2005, Ellison and Ribic 2012). For example, Ellison and Ribic (2012) documented high rates of nest defense by grassland songbirds in response to snakes using nest cameras, and Staller et al. (2005) documented nest defense at camera-monitored Northern Bobwhite (*Colinus virginianus*; hereafter "bobwhite") nests against several species of snakes and mammals. Given sufficient numbers of cameras, researchers can evaluate species-specific responses to particular predators, and their outcomes, far better than with any other current technology (e.g., Ellis-Felege et al. 2012a). The most obvious limitation of the use of cameras is that the field of view is small, such that only a portion of actual nest defenses are recorded (Pietz and Granfors 2005).

Our objective in the present study was to evaluate the role of predator identity and parental investment in decisions to engage in nest defense by incubating birds using nest cameras. Specifically, we recorded natural predator encounters to test whether predator identity, parental characteristics of age and sex, clutch investment characteristics (e.g., clutch size, days of incubation), or potential of future reproductive opportunities (i.e., time in breeding season) influenced the probability of bobwhite nest defense from camera-monitored nests in the wild. Bobwhites regularly lose a high percentage of nests to a wide array of predator species in the southeastern United States, including Raccoon, Virginia Opossum (hereafter "opossum"), Bobcat, Nine-banded Armadillo (hereafter "armadillo"), snakes, and fire ants (Staller et al. 2005; scientific names of predators are given in Table 1), which provided us an opportunity to evaluate nest defense in a multipredator community. Further, both female and male bobwhites are known to incubate nests, but typically only one or the other will incubate the nest over the 23-day incubation period (Stoddard 1931); the young leave the nest with the attending adult shortly after hatching. Clutch size of this short-lived species is highly variable, and they are capable of multiple nesting attempts in a single season (Burger et al. 1995), allowing evaluation of the importance of parental characteristics and clutch size for nest defense along with predator identity.

Given existing theory, we predicted that nest defense would be more likely when (1) predators pose little threat to adults, (2) the defending adult is female, (3) the clutch is large, (4) hatching of the clutch approaches, and (5) the encounter is late in the breeding season when re-nesting opportunities are limited. We predicted no

TABLE 1. Number of predation events, number of encounters when a Northern Bobwhite was present for the predation event, number and percentage of Northern Bobwhite responses to predators in relation to number of encounters, and average length of predator event from camera-monitored nests in southern Georgia and northern Florida, 1999–2006.

| Predator type | Number of predation events | Number of encounters | Response to predator | | | Average (\pm SE) length of predation event (min) |
|--|----------------------------|----------------------|----------------------|----------|------------|---|
| | | | Direct attack | Display | No defense | |
| Snakes (including <i>Pantherophis alleghaniensis</i> , <i>P. guttatus</i> , and <i>Lampropeltis getula</i>) | 92 | 69 | 11 (16%) | 17 (25%) | 44 (64%) | 29.8 \pm 2.8 |
| Fire Ant (<i>Solenopsis</i> spp.) | 22 | 12 | 10 (83%) | 8 (67%) | 2 (17%) | 81.1 \pm 31.4 |
| Armadillo (<i>Dasyus novemcinctus</i>) | 33 | 23 | 7 (30%) | 14 (61%) | 7 (30%) | 12.1 \pm 1.3 |
| Bobcat (<i>Lynx rufus</i>) | 18 | 17 | 0 | 0 | 17 (100%) | 12.0 \pm 1.9 |
| Raccoon (<i>Procyon lotor</i>) | 28 | 27 | 0 | 0 | 27 (100%) | 11.2 \pm 3.3 |
| Opossum (<i>Didelphis virginianus</i>) | 31 | 15 | 0 | 0 | 15 (100%) | 16.6 \pm 2.3 |
| Coyote (<i>Canis latrans</i>) | 1 | 1 | 0 | 0 | 1 (100%) | 4.0 |
| Fox Squirrel (<i>Sciurus niger</i>) | 4 | 4 | 2 (50%) | 0 | 2 (50%) | 4.0 \pm 3.0 |
| Hispid Cotton Rat (<i>Sigmodon hispidus</i>) | 2 | 2 | 2 (100%) | 0 | 0 | 2.5 \pm 1.5 |
| Feral Pig (<i>Sus scrofa</i>) | 1 | 1 | 0 | 0 | 1 (100%) | 3.0 |
| White-tailed Deer (<i>Odocoileus virginianus</i>) | 1 | 1 | 0 | 0 | 1 (100%) | 4.3 |
| Barred Owl (<i>Strix varia</i>) | 1 | 1 | 0 | 0 | 1 (100%) | 7.0 |
| Unknown | 8 | – | – | – | – | – |

effect of age on nest defense, because bobwhites are short lived, with age-independent mortality (Brennan 1999).

METHODS

Study site.—Our study area consisted of three sites in southwestern Georgia and northern Florida: Tall Timbers Research Station (Leon County, Florida; 30°39'35"N, 84°13'33"W), Pebble Hill Plantation (Thomas and Grady counties, Georgia; 30°46'22"N, 84°5'35"W), and Pinebloom Plantation (Baker County, Georgia; 31°24'42"N, 84°22'45"W). Tall Timbers and Pebble Hill are in the Red Hills region of the Coastal Plain of southwestern Georgia and northern Florida. Pinebloom is located near Albany, Georgia, in the Upper Coastal Plain physiographic region. These sites consist predominantly of old-field Loblolly Pine (*Pinus taeda*), with Longleaf Pine (*P. palustris*) and Shortleaf Pine (*P. echinata*) also present in the uplands. Pine uplands are intermixed with mesic hardwood drains or hammocks and fallow fields. Land management is representative of quail plantations in the region, with practices including annual prescribed burning, disking, roller-chopping, and mowing.

Bobwhite monitoring.—From January to April in the years 1999–2006, bobwhites were captured using baited “walk in” funnel traps (Stoddard 1931). We recorded captured bobwhites’ age and sex, and fitted each with a 6.5-g (~4% body weight) collar-style radiotransmitter (Staller et al. 2005). We assumed that radiotransmitters did not affect bobwhite nest defense (Folk et al. 2007, Palmer and Wellendorf 2007), but we acknowledge that a bird making state-dependent decisions about risk-taking may act differently with a handicap of 4% of its body mass added by the transmitter. We monitored bobwhites at least five times each week during the breeding season (15 April–1 October), and we assumed that individuals were nesting when found in the same location for two consecutive days, based on a combination of triangulation and homing. We located potential nest sites using homing

techniques (White and Garrott 1990), and we verified nesting status by visually searching for a nest when incubating individuals were off the nest during daily foraging.

Camera system.—We installed continuous-recording, near-infrared video cameras at bobwhite nests. The video camera system was composed of a N9C2 Fieldcam LRTV Microcam with a 3.7-mm wide-angle lens and an auxiliary illumination system consisting of an array of 36 light-emitting diodes (LEDs) with a wavelength of 950 nm to enable nighttime recordings (Fuhrman Diversified, Seabrook, Texas). Video data were collected by connecting a VHS time-lapse recorder to the camera and illumination system. Cameras were installed ~1.5 m from the nest bowl while the incubating parent was away from the nest. We replaced tapes and batteries every 24 h until nesting was complete or the nest was depredated. Staller et al. (2005) provide additional details of the camera setup. Because all cameras were placed the same distance from and height above each nest, the field of view was consistently ~2 m in diameter.

Data collection.—Of 790 video-monitored nests, we examined 242 predation events with bobwhite–predator interactions. We identified events on the basis of egg loss or evidence of predators (e.g., disturbed nest bowl, bobwhite abandonment) that indicated potential bobwhite–predator interactions at the nest site. We also observed additional predator interactions at the nest during a complete review of nesting video from a subset of 118 nests (847 nest-days or 20,328 h of incubation) as part of a study documenting bobwhite attendance patterns (Burnam et al. 2012). All nest observations occurred during incubation because of the difficulty of locating nests during egg laying. Following video review, we examined each predation event and recorded bird identification number, sex, age of the bird (adult–juvenile), site (property), date of predation event, predator species, predation start time and duration, period of incubation (see below), nesting period (see below), and clutch size. Time of the predation event began when the bobwhite flushed from the nest or initiated defensive action, and predation time ended with

the last camera view of the predator. We categorized the stage of incubation at the time of predation as early (days 1–8), middle (days 9–16), and late (days 17–23) according to the putative incubation start date determined by radiotelemetry location data indicating the onset of incubation. We defined nesting period as early (May–June), middle (July), and late (August–September) according to the calendar date of the depredation. Although we could occasionally identify snakes to the species level (see Table 1), we pooled all losses of nests to snakes into one category because of the lack of interspecific variation in snake predation characteristics (Staller et al. 2005). We recorded mammalian and avian predators to the species level.

For each predation event, we recorded whether or not the incubating bobwhite engaged in defensive behavior(s) against the nest predator. We defined defensive behavior as any voluntary physical engagement (e.g., active pecking of the predator) or behavioral display (e.g., feigning a broken wing) by the incubating bird against the predator. We included nonphysical engagements such as posturing (e.g., puffing up of chest or feathers, head bobbing) and pacing because they endanger the incubating bird attempting to protect the nest and its contents. We classified defensive behaviors as direct attack (e.g., rushing at the predator or making physical contact [pecking]), distraction displays (e.g., broken wing, posturing, or pacing), or a combination of these behaviors. We did not label events as “defended” or “not defended” when we could not identify the bird flushing or leaving the nest or engaging in defensive behavior.

Data analysis.—We hypothesized that the likelihood of defensive action could be influenced by a suite of characteristics that included predator type, parental characteristics, and temporal conditions. We hypothesized that bobwhites could distinguish among predators and that larger, more threatening predators would result in less defensive action than smaller predators. Previously, Staller et al. (2005) showed that meso-mammals were primary threats to eggs and adults. We had insufficient data to treat all predator species individually and, therefore, we pooled the predators into three categories: meso-mammals (i.e., armadillo, Bobcat, Coyote, Raccoon, and opossum, which served as the reference group in the statistical models), snakes, and small predators (Small Pred; i.e., fire ants, Hispid Cotton Rats [hereafter “cotton rats”], and squirrels [*Sciurus* spp.]) in a logistic regression. We excluded single predation events by White-tailed Deer, Feral Pig, and Barred Owl because of their rarity and inability to fit into our classification scheme. Further, we hypothesized that parental characteristics and clutch investment may influence defensive action in addition to predator threat level. We hypothesized (1) that the age of incubating bobwhites (juveniles [the reference] and ≥ 2 years) would not have an effect, given that bobwhites are short lived; and (2) that because of the cost of replacement of large clutches in future breeding attempts, females would be more likely to defend than males (sex; males were the reference group). We predicted (1) that the date of incubation at predation (DOI; early: days 1–8, middle: days 9–16, and late: days 17–23, with early serving as reference group) would result in increased defense as incubation progressed; and (2) that as the breeding season (Season; early: May–June, middle: July, and late: August–September with early serving as reference group) progressed, bobwhites would defend more often, given reduced future reproductive opportunities. We hypothesized that the larger the clutch

size at discovery, the more likely a bobwhite would be to defend. We constructed 36 candidate models from the individual explanatory variables and combinations of these variables thought to influence the probability of bobwhite nest defense, as well as the null model (i.e., intercept only). We evaluated these logistic regression models using SAS, version 9.3 (SAS Institute, Cary, North Carolina). We assessed goodness-of-fit using the Hosmer-Lemeshow test for the global model (i.e., model including all possible explanatory variables), and we assumed that fit was adequate when $P > 0.05$ (Hosmer and Lemeshow 1989). We calculated Akaike’s information criterion (AIC; Akaike 1973, Burnham and Anderson 2002) corrected for small sample size (AIC_c) for each predictor model to determine the simplest combination of predictors that best explained the likelihood of defense. We report the top models containing 95% of the total weight. We calculated parameter estimates for predictor variables contained in the top model with the lowest AIC value (minAIC), and we back-transformed estimates to their respective odds ratio for interpretation. Odds ratio confidence intervals including 1.0 suggest that defense is no more (or less) likely, based on a particular parameter. In addition to the analyses above, we compiled basic descriptive statistics using proportions and means to represent frequencies of various kinds of defensive behaviors that bobwhites engaged in against different predators. These details are provided to better represent behaviors that we were unable to analyze statistically and, as a consequence, do not simultaneously incorporate other predictors that influence defensive actions in bobwhites.

RESULTS

Of the 242 predation events, parents exhibited active defense at 55 (23%). We recorded three predation events at one nest, two predation events at 11 nests, and one predation event at each of the other nests. Bobwhites engaged in nest-defense behaviors against snakes, armadillos, fire ants, cotton rats, and Fox Squirrels (Table 1). We found the highest frequency of defense against fire ants (83%); however, only a small percentage of the total depredated nests was attributed to fire ants (Table 1). Most ant predation occurred toward the end of incubation as the eggs were hatching. We did not observe nest-defense behavior exhibited toward Raccoons, opossums, Bobcats, Coyotes, or the three species omitted from our statistical analyses (Fig. 1). Bobwhites were killed during seven predator interactions (six by Bobcats and one by an opossum).

We classified nest-defense behavior for 52 of the 55 active defenses employed (vegetation obstructed views for three events and prohibited their classification). Excluding ants (which were primarily pecked), broken-wing displays and combinations of direct attacks, broken-wing displays, and posturing were the primary defensive behaviors exhibited upon encountering predators (Table 1). Distraction displays (broken wing, posturing, pacing) were used alone 19 times (37% of defended nests) and in conjunction with direct attacks 20 times (38% of defended nests), often after the initial attack failed to deter the predator (Table 1). Direct attack alone was used eight times (15% of defended nests). If defensive behaviors did not discourage the predator, the attending bobwhite often would pace back and forth while the predator was raiding the nest. We observed this behavior at 17 depredated nests (33% of defended

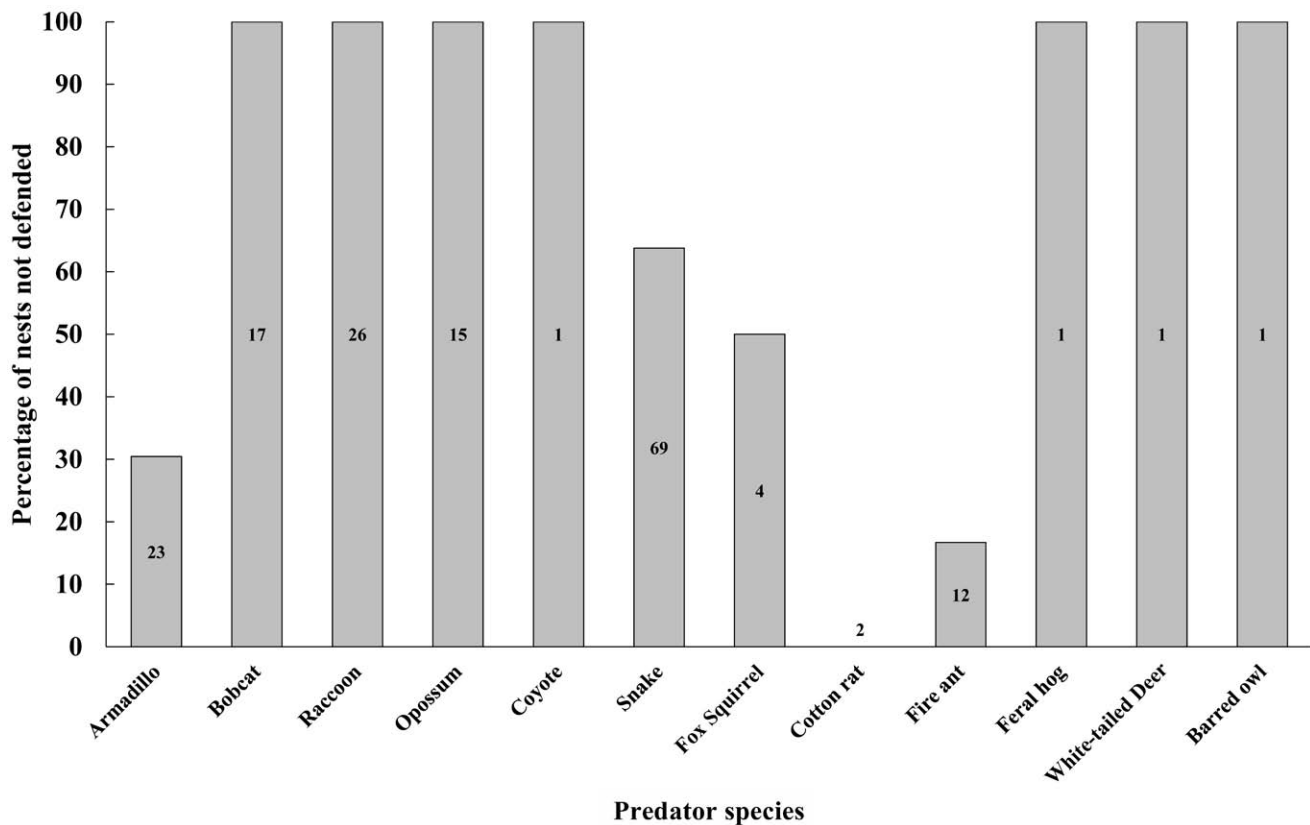


FIG. 1. Percentage of Northern Bobwhite nests that were not defended by the attending bird during predation encounters with all species detected. Numbers in each bar represent the total number of encounters with each predator.

nests). Pacing did not occur when the nest predator was a Raccoon, opossum, Bobcat, or Coyote. In events involving these species, the parent flushed immediately and returned only hours later to inspect the nest contents before abandoning the nest.

Predation events involving squirrels and cotton rats were uncommon ($n = 6$) but were usually (67%) accompanied by defensive actions. Bobwhites appear to tolerate cotton rats around their nests, given that we frequently observed cotton rats near nests within camera view, both while the parent was present and away on recess. One of the two cotton rat defenses we noted occurred late in incubation when a bobwhite returned from recess and encountered a rat in the nest bowl.

In seven cases, predators were deterred successfully from the nest without loss of eggs. Successful defenses occurred against a snake, armadillo, fire ant invasion, two squirrels, and two cotton rats. Among successful defenses, all but one was initiated by the bobwhite before the predator gained access to the nest bowl. Most frequently, the predator appeared to be startled and left immediately without a struggle. In such cases, because the predator was engaged before entering the nest, they may not have been aware of the nest and, thus, never returned. Furthermore, no successful defense involved only distraction displays such as posturing or pacing.

The best-fitting model describing probability of nest defense from our regression analysis included predator type (i.e., meso-mammal vs. Snake vs. Small Pred) and clutch size ($w_i = 0.369$) and was 1.71 \times more likely to explain the variation in the data than the second

best-fitting model, which included predator type and bobwhite age (Table 2). Further, predator type appeared in all the top five models, but only in conjunction with other explanatory variables. On the basis of our top model, bobwhites were 2.7 \times more likely to defend against snakes than meso-mammals and 14.6 \times more likely to defend against small mammals and ants (i.e., Small Pred) than meso-mammals (Table 3). However, only predator type had a 95% confidence interval in the odds ratio that did not overlap 1.0 (Table 3), which suggests that clutch size and age did not strongly influence whether a bobwhite defended the nest. Thus, we found strong support for our predicted effect of predator type, ambiguous results regarding the predicted effect of clutch size and the prediction of no effect of parent age, and no support for the predicted effects of incubation stage, time of season, and sex of the incubating adult.

DISCUSSION

Our data suggest that incubating bobwhites distinguish among the threats posed by particular predators and use that information to make the decision to flee from or actively defend the nest. Of the 11 predator species documented at bobwhite nests, bobwhites took defensive action against five. In general, bobwhites defended against predators that were capable of destroying eggs but posed little threat to the parent (i.e., ants, armadillos, snakes, cotton rats, and squirrels), and fled from predators that were a threat to adults (e.g., Raccoons, opossums, Coyotes, and Bobcats).

TABLE 2. Top candidate models (accounting for 95% of all model weights) and their number of parameters (K), Akaike's information criterion corrected for small sample size (AIC_c), ΔAIC_c , and Akaike weights (w_i) examining the probability of nest defense among Northern Bobwhites on three study areas in southern Georgia and northern Florida during 1999–2006. Explanatory variables included predator type (snake and small predators compared with meso-mammals), clutch size, age (≥ 2 years compared with first-year birds), sex (males compared with females), days of incubation (DOI; middle and late incubation compared with early), and timing in breeding season (Season; middle and late season compared with early).

| Model | K | AIC_c | ΔAIC_c | w_i |
|---|-----|---------|----------------|-------|
| Snake + Small Pred + Clutch size | 4 | 188.13 | 0.00 | 0.37 |
| Snake + Small Pred + Age | 4 | 189.20 | 1.07 | 0.22 |
| Snake + Small Pred + Age + Sex | 5 | 191.22 | 3.08 | 0.08 |
| Snake + Small Pred + Age + DOI_mid + DOI_late | 6 | 191.41 | 3.28 | 0.07 |
| Snake + Small Pred + Sex | 4 | 192.07 | 3.94 | 0.05 |
| Snake + Small Pred | 3 | 192.13 | 4.00 | 0.05 |
| Snake + Small Pred + Age + Season_mid + Season_late | 5 | 192.90 | 4.77 | 0.03 |
| Snake + Small Pred + Age + Sex + DOI_mid + DOI_late | 7 | 193.56 | 5.42 | 0.02 |
| Global Model | 10 | 193.85 | 5.72 | 0.02 |
| Snake + Small Pred + DOI_mid + DOI_late | 5 | 194.12 | 5.99 | 0.02 |
| Snake + Small Pred + Age + Sex + DOI_mid + DOI_late | 6 | 194.35 | 6.22 | 0.02 |

Small sample size forced us to lump meso-mammals into a single guild rather than run the regression on individual species. Thus, our estimates of the probability of nest defense are likely conservative for more threatening meso-mammal predators such as the Raccoon, opossum, Bobcat, and Coyote, toward which no defenses were observed, and high in relation to meso-mammals such as armadillos, against which bobwhites defended the nest in 70% of predation attempts (Fig. 1).

Bobwhites are not the only birds that differentiate between predators that are a threat to just the nest and those that are a threat to both the parent and the nest. Hatch (1997) found that responses of Song Sparrows (*Melospiza melodia*) differed according to nest predator, and that predator species determined whether the birds abandoned the nest or initiated defensive action. Dale et al. (1996) found that Pied Flycatchers (*Ficedula hypoleuca*)

TABLE 3. Minimum AIC model parameter estimates, standard error, odds ratio, and 95% confidence intervals (CI) used to explain variation in nest defense among Northern Bobwhites on three study areas in southern Georgia and northern Florida during 1999–2006.

| Parameter | Estimate \pm SE | Odds ratio | 95% CI for odds ratio | |
|---|-------------------|------------|-----------------------|-------|
| Intercept | -1.23 \pm 0.70 | | | |
| Snake (compared with meso-mammals) | 0.99 \pm 0.39 | 2.69 | 1.26 | 5.74 |
| Small Pred (compared with meso-mammals) | 2.68 \pm 0.71 | 14.56 | 3.62 | 58.61 |
| Clutch size | -0.01 \pm 0.05 | 0.99 | 0.89 | 1.09 |

never attacked model predators that were of species that could kill adults, but readily attacked model predators that were harmful only to the nestlings.

It is unclear what cues drive predator identification, but they may be based on the size of the predator (e.g., easier to see approaching), the foraging strategies that alter how the predator approaches the nest (e.g., noisier, direct approach vs. meandering approach toward nest bowl), or more likely a combination of factors. Size alone is unlikely, given that bobwhites appear to distinguish between armadillos and other meso-mammal predators (Fig. 1). To a degree, threat recognition based on predator characteristics is innate, but it may be reinforced through previous experience with different predators (Knight and Temple 1986, Montgomerie and Weatherhead 1988). Further, decisions to engage in risk-taking for the clutch may be a combination of predator threat interacting with clutch investment, such as we found with the additive effects of investment (i.e., clutch size) and parental characteristics (i.e., age) to predator identity in our top models. Nonetheless, bobwhites do not defend at all costs. The ability to double-clutch and/or re-nest enables bobwhites to buffer the loss of a nest by providing the opportunity for successful reproduction at some later point of the same breeding season (Burger et al. 1995); however, we did not find that time in the breeding season affected nest-defense decisions. Thus, the decision to defend appears to reflect the compromise between self-preservation and the perceived threat to the nest. Other work examining the distance between an approaching predator and when a bobwhite flushes suggests that bobwhites allowed predators that posed little or no risk of killing the incubating bird closer to the nest than more threatening predators (Burnam 2008).

Defense characteristics by predator type.—Distraction displays occurred alone or in conjunction with direct attacks and were the most common bobwhite nest-defense behavior. The highest frequency of defense was against fire ants, which primarily occurred toward the end of incubation as the eggs were hatching. Coincidentally, this is also when investment in the clutch is at a peak and the energetic cost of nest loss is greatest. Among events when egg loss occurred because of ant predation, most predation attempts began when the parent was away from the nest. This suggests that when a bird is present on the nest, it deters approaching ants by pecking and removing them as they arrive at the nest. When away from the nest for an extended period, ants may become present in numbers that overwhelm the nest and prevent the parent from effectively removing them. Social insects such as ants use scent trails to recruit others (Vander Meer et al. 1998), and defense behaviors such as pecking and killing of scout ants may prevent scouts from laying a scent trail from the nest to the ant colony. Hence, high nest attendance may reduce risk for egg loss from fire ants.

Among vertebrate nest predators, bobwhites defended most against snakes and armadillos. Snakes will consume adult bobwhites (Stoddard 1931), and bobwhites defended far more often against armadillos than against snakes, possibly because of the relative risks and rewards involved. By contrast, armadillos arguably pose a greater risk to the nest contents than snakes because armadillos typically ate all eggs in the clutch. Snakes often consumed only part of the clutch, so a partially snake-depredated nest could still hatch several eggs (Ellis-Felege et al. 2012b). Further, it is possible that defense frequencies against snakes and

armadillos were affected by the timing of predation. Armadillos are typically nocturnal foragers (Breece and Dusi 1985), which increases the likelihood that the bobwhites will be present on the nest and, thus, able to defend it. Many snake predation events occurred during the middle of the day when bobwhites were away from the nest foraging. Nevertheless, if we restrict the comparison to cases when bobwhites were present on their nests, we still find that only 36% of snake encounters elicited defense, whereas 70% of armadillo encounters elicited defense.

Staller et al. (2005) noted that bobwhites defended against smaller snakes (<1 m in length) more frequently than against larger snakes (>1 m in length), which suggests that larger snakes pose a greater risk to adult bobwhites. In our study, the rate of nest defense against snakes was considerably lower than the 75% found by Ellison and Ribic (2012) in grassland songbird encounters with snakes, and we suggest that this may reflect differences in the sizes and types (e.g., nocturnal–diurnal hunters) of snakes in the two studies. Unfortunately, dense vegetation prevented us from estimating snake sizes for many of the encounters.

Parental investment characteristics of defended nests.—Most studies of nest defense have tested parental investment theory without consideration of predator identity. These studies have demonstrated that nest-defense decisions can be linked to characteristics such as renesting potential, clutch age, and parental age and experience, but often these individual characteristics do not explain all of the variation and are confounded by other interacting variables (Montgomerie and Weatherhead 1988, Caro 2005). In our study, we did not find individual parental-investment characteristics (mainly described by age, sex, and clutch investment) to be important in bobwhites' decisions to engage in nest-defense behaviors. Such results agree with Caro's (2005) conclusion that empirical data on sex-specific nest defense often failed to align with theory.

Most of the studies of parental defense behavior summarized by Caro (2005) were consistent with the view that increased clutch sizes should elicit increased risk-taking by birds. Clutch size was included in our top model, but odds-ratio estimates suggested that it was not an important driver of bobwhite nest-defense behavior. Moreover, our data suggested that for each additional egg in the clutch, a bird might be slightly (1.01×) less likely to defend, which runs counter to general theory (Montgomerie and Weatherhead 1988). In agreement with our study, the studies in Caro's (2005) summary that failed to find an association between clutch size and nest-defense behavior generally identified the risk posed by predators as the primary influence on nest-defense decisions. In conclusion, we suggest that the threat posed to the clutch and the incubating parent by different predators largely drives nest-defense decisions in bobwhites, and that nest-defense-behavior in bobwhites is, at most, secondarily influenced by parental characteristics (age, sex), parental investment (clutch size, incubation stage), or probability of renesting.

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