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CHAPTER THIRTEEN

Partial Depredations on Northern Bobwhite Nests

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Abstract. Partial clutch loss following a predation event is rarely studied in ground-nesting birds despite predation often being the leading cause of nest failure. Partial nest depredation occurs when predators attack but leave some eggs intact. Using continuous video monitoring, we documented a total of 372 initial predation events at nests of Northern Bobwhites (*Colinus virginianus*). From these, we observed a sample of partial nest predation events ($n = 47$). Partial predation events resulted in three outcomes: (1) The nest failed due to parental abandonment; (2) adult stayed with the nest, but clutch failed to hatch, usually due to further predation events; or (3) adult stayed with nest and the remaining eggs hatched, adding to the reproductive fitness of the adult. Most common predators causing partial depredations were ratsnakes (*Pantherophis alleghaniensis* and *P. guttatus*), kingsnakes (*Lampropeltis getula*), and fire ants (*Solenopsis* spp.). We used logistic regression and model selection methods to assess six cues that parents may use to determine the value of remaining offspring and resulting abandonment decision. Overall, nests with fewer eggs remaining after the predation event or those predated early in the incubation period were more likely to be abandoned; juveniles appeared more likely to abandon than adults. Future studies will be needed to confirm our findings of the relationships between cues and abandonment decisions, and video surveillance systems will be a necessary component of these studies.

Key Words: AIC, *Colinus virginianus*, Florida, Georgia, logistic regression, Northern Bobwhite, partial depredation, predators.

In many birds, especially ground-nesting species, predation is the leading cause of nest failure. Not all nest predation events, however, lead to the complete loss of the nest. Partial depredations occur when a predator chooses (e.g., predator is satiated) or is forced (e.g., nest defended by the attending bird) to consume only part of the clutch of eggs, thus leaving some eggs intact with the potential to successfully hatch (Ackerman et al. 2003a). Partial depredations have been documented and occur frequently in several waterfowl species (Choate 1967, Lariviere and Messier 1997, Ackerman et al. 2003a). Partial clutch loss in many avian species is now thought to occur more often than realized in the past (Robinson and Robinson 2001). However, for most avian species partial depredations are rarely examined to determine their frequency, their role in overall

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production, the cues that influence parental decisions, and/or predators responsible for reducing the clutch.

Following a partial predation event, birds may choose to abandon their nest or continue incubation, which may or may not lead to a successful nest with reduced brood size (Ackerman et al. 2003a). Analysis of nest and brood abandonment is becoming a common way to study parental care behaviors (Ackerman and Eadie 2003; see review by Szekely et al. 1996). Abandonment following partial depredations provides the opportunity to study potential cues that drive parental behavior decisions because these events may occur at any stage in the breeding season or incubation stage and result in a variety of remaining clutch sizes (Ackerman et al. 2003b).

Parental investment is any behavior by the parent that increases the offspring's chance of surviving at the cost of future offspring opportunities for the parent (Trivers 1972). The theory predicts that parents should make decisions that maximize their lifetime reproductive success by balancing the trade-off between current and future reproduction (Trivers 1972). Nest depredation for birds can be the single most important variable affecting fitness (Ricklefs 1969). Therefore, a bird's decisions following partial clutch loss are critical to its overall fitness, and the cues that drive these decisions are of importance for understanding the trade-offs between current and future reproduction and productivity gains and losses as a result of partial clutch depredations. However, it often is challenging to separate whether individuals use past investment or expected benefits to make parental care decisions since these simultaneously change throughout the reproductive process (Ackerman and Eadie 2003).

There are many potential cues that may increase the probability of the bird abandoning a nest rather than returning to incubate the remaining eggs. Some of the cues are characteristics of the parents such as age and sex. The sex of the parent plays a role if there are differences in confidence of parenthood, renesting potential, perception of risk, and the ability to raise young unaided (Montgomerie and Weatherhead 1988). The age of the attending adult could influence the probability of a bird abandoning, where older birds would have fewer future opportunities and thus are more likely to remain with a nest, particularly if the probability of survival is low (Montgomerie and Weatherhead 1988). Other cues have to do with the partial predation event, such as remaining clutch size, when the predation event occurred during the breeding season (Bruning 1973, Montgomerie and Weatherhead 1988, Szekely et al. 1996), and the species of predator. Clutch size attributes, such as the proportion of the clutch lost, likely influence parental decisions based upon investment in the clutch, as well as the expected benefit of the clutch (Ackerman et al. 2003b). Timing of the predation event during the breeding season and abandonment may be reflective of renesting potential; early season nests may not be worth as many risks as nests at the end of the breeding season, where a parent would have to survive until the next breeding season for the next opportunity for reproduction (Montgomerie and Weatherhead 1988). Additionally, the stage in incubation at which the predation event occurs could influence parental care decisions (Rosene 1969, Ricklefs 1973, Sjoberg 1994, Mallory et al. 1998, Ackerman et al. 2003b). Offspring become more valuable as the clutch ages; therefore, later in incubation a bird should be less likely to abandon the nest based upon the increased parental investment (Ricklefs 1973, Barash 1975). Individual predator species have a variety of search strategies and pose different types of risks both to the attending bird and to the clutch (Gochfeld 1984), thereby also influencing parental investment decisions.

The Northern Bobwhite (*Colinus virginianus*) provides a unique study system since one adult representing either sex may incubate a particular nest, but only one of them typically will incubate an individual nest, with each having different reproductive costs at stake should the nest fail (Burger et al. 1995). Little is understood as to how decisions are made about which parent incubates, but it has been suggested that it may be related to an unequal sex ratio limiting breeding opportunities for males unless they increase participation in the nesting process (Burger et al. 1995). Bobwhites also are persistent renesters, indeterminate layers, and may have multiple broods during a breeding season. Average clutch size for bobwhites is 12–14 eggs/nest and decreases as the nesting season progresses (Brennan 1999). They are a ground-nesting species, making them extremely vulnerable to predation, particularly from meso-mammals and snakes.

There is a diverse predator community that preys upon bobwhite nests including, but not limited to, raccoons (*Procyon lotor*), nine-banded armadillos (*Dasypus novemcinctus*), opossums (*Didelphis marsupialis*), bobcats (*Lynx rufus*), red and gray fox (*Vulpes vulpes* and *Urocyon cinereoargenteus*), coyotes (*Canis latrans*), skunks (*Mephitis mephitis*), snakes [particularly ratsnakes (*Pantherophis alleghaniensis* and *P. guttatus*) and kingsnakes (*Lampropeltis getulus*); taxonomy from Crother 2008], and fire ants (*Solenopsis* spp.) (Stoddard 1931, Staller et al. 2005, Rader et al. 2007). These species interact with the bird and its nest in different ways. Staller et al. (2005) and Burnam (2008) reported that some predators of bobwhite nests always completely destroyed the nests and often attempted to kill the attending adults. They also reported that attending bobwhites defended the nest against some predator species but not others. For some species, such as snakes, attending bobwhites often defended the nest against small individuals but abandoned their nests when attacked by larger snakes (Staller et al. 2005). The type and characteristics of a predator, then, may affect decisions made by bobwhites during and after nest predation events.

Until recently our ability to monitor avian nests to assess individual predation events has been limited and required considerable logistics to observe predation events. Identification of the predator species from sign at the nest following a predation event is not a reliable method (Williams and Wood 2002, Staller et al. 2005). However, use of miniature video surveillance systems has allowed investigation of fine-scale behaviors at natural nests. Researchers can examine the response of birds to actual predator species, as well as the danger different predators pose to the nest and incubating adult, providing insight on how predator-specific factors influence reproductive decisions (also see Ellison and Ribic, chapter 12, this volume).

In this paper, we discuss possible cues influencing abandonment decisions from Northern Bobwhites nests monitored using video surveillance systems. We evaluate parental investment cues related to parental and clutch characteristics, as well as the predators responsible for partial clutch loss, to determine which cues may drive abandonment decisions.

METHODS

Study Area

We studied bobwhite nesting at three sites in southern Georgia and northern Florida during 2000–2006. Two sites were located in the Red Hills physiographic region on either side of the state line. Pebble Hill Plantation is in Grady and Thomas counties, Georgia (30°46′22″N, 84°5′35″W), and Tall Timbers Research Station and Land Conservancy is in Leon County, Florida (30°39′35″N, 84°13′33″W). The third site, Pinebloom Plantation, is in the Upper Coastal Plain physiographic region in Baker County, near Albany, Georgia (31°24′42″N, 84°22′45″W). Detailed site description for the Red Hills sites can be found in Staller et al. (2005), and for Pinebloom in Sisson et al. (2000, 2009). All three sites are managed using frequent fire, disking, roller-chopping, and mowing to maintain an open, low-density pine forest structure. Sites are dominated by loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*), with associated "oldfield" ground cover vegetation and areas of longleaf pine (*Pinus palustris*) with associated wiregrass (*Aristida stricta*) ground cover. Hardwood drains, hammocks, and fallow fields are interspersed across the landscape. These sites and the surrounding areas have stable populations of bobwhites.

Field Methods

Each year during January, bobwhites were captured using funnel bait-traps (Stoddard 1931) and fitted with 6-g collar-style radio transmitters. Trapping, handling, and marking protocols followed those required in our University of Georgia Institutional Animal Care and Use Committee permit #A2004-10109-c1 and A3437-0. Bobwhites were located at least five days per week to monitor nesting behavior between 15 April and 1 October of each year. Birds found in the same location on two consecutive days were assumed incubating, and initiation of incubation was based upon these telemetry methods. Flagging was placed on vegetation above, but near, the nest site to mark its location and was done in a standardized fashion for all nests. When the radio-tagged bobwhite was away from the location, researchers located the exact nest position, counted eggs, and installed near-infrared cameras (Furhman Diversified, Seabrook, TX). A small camera with a near-infrared (950 nm) lighting source was placed approximately 1–1.5 m from each nest (Staller et al. 2005). Surrounding vegetation was used to camouflage the cameras. The cameras were linked via a 25-m cable to VHS recorders and 12-V, deep-cycle marine batteries. Recorders were modified to operate at 1/3 speed, resulting in 10 frames per second and allowing an 8-hour tape to last 24 hr. Tapes and batteries were replaced daily.

Nests were checked daily until failure or hatch via telemetry to determine if the incubating parent was at the nest. In the event the parent was not present, the nest was physically checked to determine if the nest was intact and the parent was away on recess, if a predation event had occurred, or if the nest had hatched. Throughout the incubation periods, subsequent clutch counts were conducted when the bobwhite telemetry indicated that the attending adult was on recess. Partial egg loss was determined from a decrease in eggs during subsequent egg counts from the initial clutch size. Additionally, abandonment was considered to occur from clues such as the incubating adult not being present at the nest or egg temperatures indicating that ongoing incubation had not occurred recently. If we were uncertain about the fate of the nest, we revisited the nest later in the day or on the subsequent day to confirm its fate. Videos were viewed to identify the nest predator in the event of a partial reduction in clutch size during the incubation period. In the event that multiple predation events occurred, only the first predation event was used in this analysis.

Statistical Analysis

We summarized the predators responsible for the partial depredations by feeding/foraging guilds. We tested for differences in percentage of eggs remaining and date of predation event for the major species groups by examining 95% confidence intervals.

We modeled the probability of nest abandonment using logistic regression. Six explanatory variables were used (see Table 12. 1 for detailed rationale): day of incubation (DOI); Julian Date for time in the breeding season when the

TABLE 13.1

*Explanation of predictor variables used to assess the probability of abandonment following partial depredation events at Northern Bobwhite (*Colinus viginianus*) nests monitored in northern Florida and southern Georgia during 2000–2006.*

Variable	Explanation
Per_eggs	Describes proportion of eggs remaining after the partial depredation event. Studies suggest that abandonment is correlated with high proportions of clutch loss (Ackerman et al. 2003b, Hall 1987).
Pred	Describes predator responsible for the partial nest depredation. A bird may assess the value of the nest based upon future risk of depredation or its own survival based upon the predator responsible for the event.
TBS	Describes the timing in the breeding season based upon Julian Date when the depredation occurred. Studies suggest that early nests may be more likely to be abandoned if there is enough time to renest.
DOI	Describes the day of incubation (i.e., clutch age) at the time of the depredation event. The clutch becomes more valuable as it ages because of the increasing parental investment and increasing probability of a successful hatch.
Age	Describes the age of the attending bobwhite as a juvenile (first breeding season) or an adult (≥ second breeding season). Older birds will be less likely to abandon because they have limited future breeding opportunities.
Sex	Describes the gender of the attending bobwhite. Males with unknown clutch paternity would be incurring large reproductive costs. Females would be less likely to abandon given the cost of laying the clutch and the confidence in maternity.

predation event occurred (TBS); percent of eggs remaining after a predation event (per_eggs); predator guild [fire ants, snakes, unknown (predator could not be identified), and mammals]; and age (juvenile or adult) and sex of the attending bird. Juvenile birds were defined as bobwhites entering their first breeding season, and adults were those who had survived at least one previous breeding season. Fire ants were used as the baseline of comparison for the other predator groups.

We created a set of *a priori* models for these predictors individually and as additive models in combination with one another. Pearson correlations were run on all pairs of predictor variables. To avoid multicollinearity, variables with correlations greater than 0.45 were considered correlated and not used in the same regression model. This resulted is 24 candidate models, including the constant model where only the intercept was modeled.

A Hosmer–Lemeshow goodness-of-fit test was conducted on the global model to determine if an adequate fit was observed (Hosmer and Lemeshow 1989). We also examined $\hat{c}$ to determine if the data were overdispersed (Lebreton et al. 1992). To rank the models, we used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) (Burnham and Anderson 2002). We used model weights to determine how much better the minimum AIC model was than the other models (Burnham and Anderson 2002). Model-averaged estimates from the entire candidate model set were calculated for the predictor variables (Burnham and Anderson 2002, Anderson 2008). The model-averaged odds ratios were calculated for the parameter estimates and scaled to biologically meaningful values for interpretation. For example, a scalar unit of 1 means a binomial variable, whereas DOI and TBS in our data are scaled by 7-day units. In addition, we graphically explored proportions of abandonment relative to the predictor variables of interest and calculated Bonferroni 95% confidence intervals around these estimates (Byers et al. 1984). For the graphs, we binned the explanatory variables to clearly illustrate the relationships at biologically meaningful time scales (e.g., early, middle, late breeding season). All analyses were conducted using SAS (ver. 9.1, SAS Institute 2003).

RESULTS

We monitored 749 bobwhite nests. Of those, there were 285 (full) and 87 (partial) initial predation events. Males incubated nine (19.1%) of the nests, and females incubated the other 38 (80.9%). Following partial clutch loss, 40.4% of nests were abandoned by the attending bobwhite. Twenty of the 28 (71.8%) nests where birds returned to continue incubating the nest resulted in the success of at least some of the remaining clutch.

We had 47 nests where the predation event was captured on camera and usable for further analysis. Some of the partial predation events were only known to occur because of reduced clutch size. This occurred in some cases because we did not have cameras in place from the onset of incubation, and clutch loss occurred before camera installation occurred. In addition, slight variations in camera angles such as to the side rather than directly in front of the nest opening were used. This meant that there were limitations in viewing all angles of the nest. Some predators would enter from the rear or side of the nest, limiting our ability to detect their presence.

The most common predators identified partially depredating bobwhite nests were corn snakes, ratsnakes, and kingsnakes (n = 22), and fire ants (n = 10). Virginia opossum (*Didelphis virginiana*), hispid cotton rat (*Sigmodon hispidus*), and white-tailed deer (*Odocoileus virginianus*) each partially depredated a single bobwhite nest. At 12 nests, the predator could not be identified due to thick vegetation. These unknown partial depredations were likely snakes or ants, which were the most common predators and often difficult to view in the thick vegetation surrounding bobwhite nests.

Egg loss, which could be misinterpreted as a partial nest depredation, was observed during nest maintenance on three occasions, although one was associated with an earlier attempted predation event. We observed two female and one male bobwhite carry a single egg from their nests. The first observation was a male bobwhite which began pecking and rolling eggs in the nest. One minute later the bobwhite picked up the egg and flew out of the nest carrying it. The second event observed involved a female bobwhite. She was observed moving into the nest following a recess event, then promptly ran out of the nest carrying an egg, and continued out of the camera view. On the previous day, this bird had been observed defending her nest against attack by ants. The final observation of a bobwhite carrying an egg was a female bobwhite that emerged from her nest carrying an egg and flew away with it in her beak. In all observations, the bobwhite appeared to be carrying the egg with the lower mandible inserted into a hole in the egg. Based on camera observations, it could not be determined if the bobwhite created the hole or the egg had previously been damaged.

Among predation events, we also identified temporal differences among predator species relative to incubation period. For the two groups most involved in partial predation events, we observed nonoverlapping 95% confidence intervals; mean day of incubation for predation events by snakes was 11.8 (95% CI: 8.9–14.7), whereas for ants, mean day of depredation was 17.8 (95% CI: 15.0–20.6). Although the 95% confidence intervals overlap, there is a trend toward more eggs remaining after ant predation events than after snake events. Average percent of eggs remaining after an ant depredation was 66.8% (95% CI: 50.2–83.4%) compared to 48.6% (95% CI: 39.5–57.7%) remaining following snake depredations.

The Hosmer–Lemeshow goodness-of-fit statistic for the global model indicated logistic regression was an adequate fit for the data set (P = 0.26). Data demonstrated overdispsersion ($\hat{c}$ = 1.42); therefore an adjustment was made to correct the overdispersion and an additional scaling parameter was added to each of the models. All but two models possessed at least some weight, with 95% of weight carried by 13 of the models (Table 13.2). The best approximating model for predicting bobwhite abandonment following partial clutch loss included the predictors of age, date of incubation, and percentage of eggs remaining, while the next best fitting model included only date of incubation and percentage of eggs remaining (Table 13.2).

Percentage of eggs remaining following partial clutch loss and date of incubation were the variables that appeared to best describe the probability of bobwhite abandonment following a partial depredation (Table 13.2). While the scaled odds ratios had 95% confidence intervals which encompassed 1, date of incubation and percent eggs remaining exhibited asymmetrical confidence intervals, showing a predominantly negative influence (Table 13.3). Model-averaged estimates for the percentage of eggs remaining (Table 13.3) indicated that for every additional 30% of the clutch remaining following a partial depredation, the attending bobwhite was 3.1 times less (or 0.32 time more) likely to abandon the nest (Fig. 13.1). For each additional week progressed in incubation, the bird was 4.0 times less likely to abandon the nest (Fig. 13.2). Age appeared to have some effect on abandonment. Adult bobwhites were 9.6 times less (or 0.10 times more) likely to abandon than juvenile bobwhites in their first nesting season (Table 13.3). The other explanatory variables did not appear to influence abandonment (Tables 13.2 and 13.3). We note that the observed broad confidence intervals surrounding most of the parameter estimates are likely the result of small sample sizes.

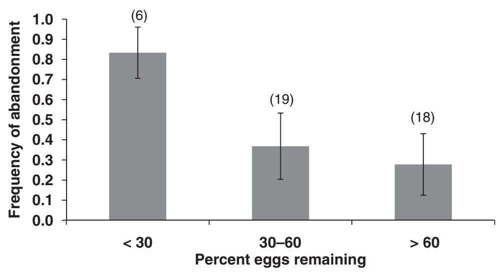

Figure 13.1. Frequency of nest abandonment (± 95% confidence intervals) by attending Northern Bobwhites (*Colinus virginianus*) following partial depredation events by percentage of eggs remaining after event. Scalar unit of analysis was 30%.

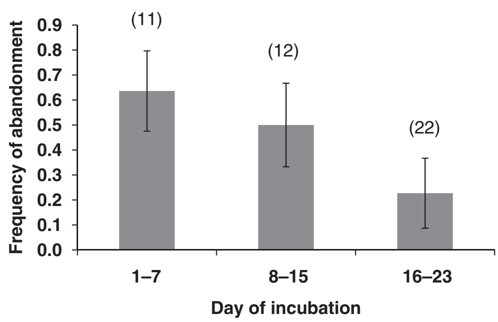

Figure 13.2. Frequency of nest abandonment (± 95% confidence intervals) by attending Northern Bobwhites following partial depredation events by day of incubation. Scalar unit of analysis was 7 days.

TABLE 13.2

AIC_c model selection for 24 candidate models examining cues bobwhite use in deciding whether to abandon a nest following partial clutch loss.

Model	K	Dev	ΔAIC_c	w_i
Age + DOI + per_eggs	5	18.916	0.000	0.293
DOI + per_eggs	4	22.339	0.762	0.200
Age + Sex + DOI + per_eggs	6	17.920	1.760	0.122
per_eggs	3	26.829	2.814	0.072
Age + DOI	4	24.669	3.038	0.064
Age + per_eggs	4	24.797	3.277	0.057
DOI	3	28.903	4.830	0.026
Age	3	28.904	4.859	0.026
Constant (intercept only)	1	31.453	5.095	0.023
Sex + per_eggs	4	26.802	5.224	0.022
Age + DOI + TBS	5	24.599	5.507	0.019
Age + Sex + DOI	5	24.641	5.549	0.018
Sex	3	30.645	6.572	0.011
Sex + DOI	4	28.310	6.632	0.011
Age + Sex	4	28.774	7.144	0.008
DOI + TBS	4	28.903	7.225	0.008
TBS	3	31.349	7.277	0.008
Age + Sex + DOI + TBS	6	24.583	8.163	0.005
Pred + per_eggs + DOI	5	22.129	8.698	0.004
Pred + per_eggs	4	26.421	10.124	0.002
Pred	3	31.072	11.905	0.001
Pred + DOI	4	28.739	12.209	0.001
Age + Sex +DOI + TBS + Pred + per_eggs	8	17.439	14.141	0.000
Age + Sex + Pred	5	28.699	15.096	0.000

NOTE: Predictor variables are age and sex of incubating bobwhite, timing in the breeding season (TBS), day of incubation (DOI) when the depredation event occurred, percent of eggs (per_eggs) remaining, and predator (Pred).

DISCUSSION

Even with our large sample of nests monitored, we demonstrate that investigation of specific behaviors in nesting studies are still difficult to accomplish even with video monitoring. Our findings may not be as strong as we would like about the relationship of specific cues to bobwhite abandonment following partial depredations, but there have not been any other camera studies to our knowledge focusing on partial depredations in ground-nesting birds with indeterminate clutches. Our results suggest that some cues deserve further consideration and examination and are better than the intercept-only model. Our findings suggest that bobwhites may use multiple cues to assess the value of a clutch and reproductive decisions following partial depredation, as no single cue which we examined was driving their decisions. Of the predictors we examined, day of incubation and percentage of eggs remaining appear to play a role in the bobwhite's decision to either abandon the nest and try to renest or to salvage the effort invested in the partially depredated nest. Researchers studying waterfowl have found

TABLE 13.3

Model-averaged parameter estimates for bobwhite abandonment following partial clutch loss and their associated scaled odds ratios.

Parameter	Estimate	SE	Odds ratio	Unit scalar	Scaled odds ratio	95% CI for scaled odds ratio	
						Lower	Upper
INTERCEPT	3.663	3.280					
AGE	−2.264	1.769	0.104	1	0.104	0.003	3.331
SEX	−1.032	2.042	0.356	1	0.356	0.007	19.511
DOI	−0.199	0.114	0.820	7 days	0.249	0.052	1.184
TBS	0.002	0.015	1.002	7 days	1.012	0.821	1.247
PREDATOR:							
UNKNOWN	0.346	1.575	1.413	1	1.413	0.064	30.948
SNAKE	0.088	1.566	1.092	1	1.092	0.051	23.505
MAMMAL	−0.171	2.505	0.843	1	0.843	0.006	114.263
PER_EGGS	−0.038	0.028	0.963	30%	0.319	0.061	1.665

NOTES: Odds ratios$>$1.0 indicate a positive response relative to a unit scalar change; $<$1.0 is a negative response. Scaled odds ratios represent the likelihood of change relative to a biologically significant unit change. Predator estimates are relative to ants.

similar results. Ackerman and Eadie (2003) found that both day of incubation and the proportion of eggs remaining were important predictors in Mallard (*Anas platyrhynchos*) nest abandonment. Hall (1987) also observed higher nest abandonment at mallard nests with a greater proportional clutch loss.

Although waterfowl are also ground nesters with indeterminate clutches, parental investment is likely quite different from bobwhites because of other life history traits. Specifically, the attending bobwhite's age appeared to carry some weight. Given the short lifespan and high annual mortality that bobwhites experience (Stoddard 1931, Brennan 1999), a bobwhite might be more likely to take greater risks in their second breeding season than their first because there may be limited opportunities for future offspring (Montgomerie and Weatherhead 1988).

Interestingly, most predation events by ants occurred later in incubation but resulted in a greater proportion of the clutch remaining. Fire ants were unable to directly access eggs unless they were damaged or hatching. Since many of the attempts occurred later in incubation, but not always at hatch, only a few eggs were typically lost due to lack of access to the egg. When the incubating bobwhite is present at the nest, it will aggressively defend against ants within the nest (Burnam 2008). Based upon our camera observations, we believe that eggs may be damaged during defense or as a result of predator disturbance. This may result in access to the egg by ants and ultimately partial clutch loss. However, the incubating bobwhite, as we observed, may be removing the damaged egg to increase the probability of success for the remaining eggs in the clutch (Kemal and Rothstein 1988). Studies conducted on partial depredations traditionally use a decrease in clutch size (Ackerman and Eadie 2003; Ackerman et al. 2003a, 2003b) as evidence of partial predation events. However, our camera observations suggest that not all clutch loss is the direct result of predation, but rather has been suggested to be a response to damaged or infertile egg(s) (Robinson and Robinson 2001).

Our lack of strong relationships between the cues used in our study and bobwhite abandonment may also suggest that other cues may be driving bobwhite parental care decisions relative to partial clutch loss. For example, bobwhites are persistent renesters and often hatch multiple broods within a breeding season. Investments in terms of how many previous attempts have been made and the success of those attempts may influence the risks a bobwhite is willing to take following partial predations events at current nests. Evaluation of predation risk may be influenced by specific features associated with nesting habitat, such as nest location on the landscape and concealment. Ackermann et al. (2003b) also suggested that clutch size attributes can be examined in several ways. For example, the initial value of eggs or the absolute number of eggs remaining may better reflect how a bird evaluates reproductive investment and potential gains (Ackermann et al. 2003b).

In assessing recruitment and other parameters relative to population dynamics of bobwhites, our results suggest that traditional approaches using nesting success where at least one egg hatches does not account for the amount of production gained or lost as a result of partial depredations (also see Pietz et al., chapter 1, this volume), and additional information related to egg success would provide additional information on production (Ackerman et al. 2003a). The relative contribution of particular species to both full and partial depredations, as well as temporal factors such as predation events during early or late incubation, lead to different production gains that require more detailed measures. Future research needs to address production and the specific role of predators with respect to partial clutch loss at bobwhite nests.

In summary, our findings suggest that bobwhites use multiple cues to assess the value of a current clutch following partial depredations. The proportion of the clutch lost appears to be an important factor in conjunction with clutch age and to some extent the age of the attending bobwhite. Partial depredations are important from both an applied and a theoretical perspective, and there is a need for a better understanding of the role they play in production and reproductive decisions of avian species. In addition, our camera system represented a major opportunity to assess behaviors of bobwhites resulting from predation events that were previously only available through anecdotal evidence.

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