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Patterns of Incubation Behavior in Northern Bobwhites (*Colinus virginianus*)

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Abstract. Patterns of incubation and nesting behavior for many species of birds, especially those with cryptic nests, have been difficult to obtain due to logistical and technological limitations. As a result, little is known about the daily attendance rhythms and behavioral patterns of many species, including the Northern Bobwhite (*Colinus virginianus*), despite this species being one of the most studied birds in the world. Incubation represents parental investment in offspring, and a multitude of factors may affect investment behaviors, including reproductive ecology, sex and age of parent, habitat quality, clutch age, and timing in the nesting season. Most Northern Bobwhite nests are incubated by a single adult, most often by females, but also by some males. We assessed the nest attendance patterns and parental investment in bobwhite clutches ($n = 118$) using continuous near-infrared video of nests being incubated by male or female bobwhites. We found that incubating parents took 0–3 recesses per day. A single recess was most common for 87% of nest-days, and most of these were during mid-day to late afternoon (12:00–19:00). Mean total daily recess time was 182 min (95% CI: 98–264) for nests that hatched and 224 min (95% CI: 140–308) for nests that failed. We observed no difference between sexes in the number or length of recesses taken, but females initiated recess later in the day (median start time = 15:00) than males (median start time = 14:00). We found that nest recess length decreased as the clutch got older and increased as the nesting season progressed. Video surveillance systems proved to be a useful tool for observing and quantifying patterns of incubation behavior in a ground-nesting species with cryptic nests.

Key Words: AIC, attentiveness, *Colinus virginianus*, Florida, Georgia, mixed models, Northern Bobwhite.

P arental investment during nesting involves a number of physiological and behavioral parameters that influence the likelihood that offspring will survive. Incubation entails protection of eggs during development, most commonly thought of as warming the embryos to proper temperature for development, but might also include cooling of eggs and protection of eggs from predators. Many ground-nesting species of Galliformes, including the Northern Bobwhite

(*Colinus virginianus*; hereafter, bobwhite), are difficult to observe; therefore, most observations of incubation behavior are individual and anecdotal (Stoddard 1931). Because of the well-documented bobwhite decline (Church et al. 1993, Brennan 1999), a great deal of research has been directed toward understanding bobwhite ecology. Consequently, bobwhites are one of the most studied species in the world (Guthery 1997, Williams et al. 2004). However, little is known about specific bobwhite incubation behaviors.

Parental investment is an underlying mechanism that influences incubation behavior. Trivers (1972) defined parental investment as any investment by the parent that increases the likelihood of offspring survival while decreasing the parent's ability to invest in other offspring or activities. A multitude of factors may affect incubation behaviors, including reproductive ecology, sex and age of the parent, habitat quality, clutch age, and timing in the nesting season (Trivers 1972, Moller 1991, Rauter and Reyer 1997).

The energetic costs of incubation are high for many avian species (Monaghan and Nager 1997), and nest attendance is likely constrained by the depletion of energy reserves (Cresswell et al. 2004). Because an individual has only finite resources available, the energetic cost of reproduction may impact the success of the current attempt or the potential for future nesting attempts (Stearns 1992). As a result, incubation strategies are frequently a tradeoff between meeting the metabolic needs of the parent, minimizing predation risk, and maintaining a suitable environment for developing embryos (Afton 1980, Flint and Grand 1999). An attending bird's ability to balance daily energetic needs with incubation requirements is a continuous trade-off influenced by individual physical characteristics of the parent, environmental conditions, and daily and seasonal factors (Lorenz 2005). If there is a reduction in these daily energetic costs, the parent may be able to invest more in the nest through increased attentiveness (Bryan and Bryant 1999).

Although energy reserve levels and the energetic constraints imposed by incubation may limit attendance, time spent in nest recess may vary widely even among conspecifics nesting in the same area at the same time, as well as those of different species. Gloutney et al. (2004) found that recess times for individuals of both Ross's and Lesser Snow Geese (*Chen rossii* and *C. caerulescens*, respectively) varied widely depending on reproductive stage and food intake. Likewise, incubation initiation has been shown to vary among conspecifics with regard to individual body condition and egg size (Hanssen et al. 2002).

Bobwhites are a cryptic, ground-nesting species. Although primarily uniparental incubators, nests may be incubated by either the male or female parent, with up to 25% of males incubating in a given season (Burger et al. 1995). Stoddard (1931), using direct observation of a limited number of nests, noted that bobwhites generally recessed 2–3 times daily, usually in the afternoon for varying lengths of time, but these observations were not correlated with parental and temporal characteristics.

The objective of our paper is to discuss and quantify the potential factors influencing nest attentiveness and recess patterns in Northern Bobwhites using video technology. We examined a range of potential factors including sex and age of the incubating parent, clutch age and size, and seasonal correlates. We predicted that incubation recess duration would be a function of the trade-off between reduced recess length for predator avoidance and increased length as a result of the incubating bird fulfilling their energy intake requirements.

METHODS
Study Site

Our study area consisted of three sites; Tall Timbers Research Station (Leon Co., FL; 30°39′35″N, 84°13′33″W), Pebble Hill Plantation (Grady and Thomas Co., GA; 30°46′22″N, 84°5′35″W), and Pinebloom Plantation (Baker Co., GA; 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 Plantation is located near Albany, Georgia, in the Upper Coastal Plain physiographic region. These sites consist predominantly of old-field loblolly (*Pinus taeda*), with longleaf pine (*P. palustris*) and shortleaf pine (*P. echinata*) also present in the uplands. The pine uplands are intermixed with mesic hardwood drains/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 (Stoddard 1931, Brennan 1999, and

Staller et al. 2005). Fall covey counts estimated early fall bobwhite densities to be approximately 2.2, 1.0, and 3.7 birds per ha on Tall Timbers, Pebble Hill, and Pinebloom, respectively (Thornton 2003).

During 1999 to 2006, bobwhites were captured from January to April using baited "walk in" funnel traps (Stoddard 1931, Smith et al. 1981). Captured bobwhites were classified by age and sex, and fitted with 6.5-g pendant-style radio transmitters (Staller et al. 2005). Capture and handling procedures followed the guidelines presented in the American Ornithologists' Union Report on the Use of Wild Birds in Research (American Ornithologists' Union 1988), as well as the University of Georgia Institutional Animal Care and Use Committee (Permit #A34337-01 and #A199-10028-N2). Bobwhites were monitored ≥5 times/week between 15 April and 1 October each year and assumed to be nesting when in the same location for two consecutive days. Nests were then located using telemetry homing techniques (White and Garrott 1990).

Camera System

When telemetry techniques indicated the incubating bobwhite was away on a recess period, we installed continuous-recording, near-infrared video cameras 1−1.5 m from the bobwhite nest bowl. The video camera system was comprised of a N9C2 Fieldcam LRTV Microcam with a 3.7-mm wide-angle lens (Furman Diversified, Inc.). Sunlight provided sufficient light for daytime recording, and nighttime recording was supported by an auxiliary 36-array LED infrared illumination system at 950 nm. Both components were supported on a camouflaged articulating arm attached to a wooden stake. The camera and illumination system were connected to a VHS time-lapse recorder that continuously recorded 10 frames/sec, located approximately 25 m from the nest. Because the recording rate was 1/3 normal speed, each 8-hr tape lasted 24 hrs (Staller et al. 2005). The camera system was powered by a 12-V marine battery located next to the VHS recorder. Nests were monitored throughout incubation.

Care was taken to minimize disturbance of the area, including situating cables and cords so as not to cross likely predator travel routes such as firebreaks and roads (Staller et al. 2005). After installing the camera, the nest was monitored every 2 hrs to ensure the bird returned to resume incubation. A technician replaced VHS tapes and batteries every 24 hrs until nesting was complete or the nest was depredated.

Data Collection

We selected a random sample of 118 nests (male = 56, female = 62) from a total of 782 monitored bobwhite nests and viewed the nest video for each incubation day of every bird selected. For each camera-day, we recorded the bird's identification number, sex, age, study site, date, number of recesses taken (if any), recess start time and duration, period of incubation (clutch age), nesting period, and clutch size. Recess start time was recorded as beginning when the bobwhite first left camera view of the nest, and ended when the bobwhite returned to the nest bowl. Movements of the attending bird lasting <1 min were not considered recess events because we often observed attending adults standing and moving around the nest to adjust eggs. We categorized period of incubation as early (days 1−8), middle (days 9−16), or late (days 17−23). Period of incubation was calculated by back dating from the day of hatch for successful nests (assuming a 23-day incubation period); for failed nests, period of incubation was assigned according to the date that telemetry observation indicated the bird was stationary and incubating. We used incubation period rather than day because we know that there can be some error in estimation of initiation of incubation date. In addition, events, such as thunderstorms, can drastically impact behavior over a daily time period; however, we could not assign impact even on the spatial scale we were working. Likewise, nesting period was defined as early (May−June), middle (July), and late (August−September) according to the date of the observation. For each recess event, we noted the method by which the bobwhite left the nest (flush or walk), as well as general weather conditions, such as rain and high wind.

Data Analysis

We believed frequency and duration of daily nest recess could potentially be influenced by a suite of parental characteristics and temporal conditions. Thus, we used a mixed model

analysis to analyze the effect of covariates on daily recess length (Coates and Delehanty 2008). We constructed hierarchical models using the PROC MIXED procedure from SAS software (SAS Institute 2003). PROC MIXED allows for the incorporation of repeated measures into the candidate models and allowed us to avoid pseudoreplication caused by assuming that repeated observations on the same bird were independent (Hurlbert 1984, Coates and Delehanty 2008).

Our global prediction model consisted of CLUTCH (clutch size), SEX (sex of incubating parent), AGE (age of incubating parent), POI (period of incubation on the day of recess), and SEASON (stage of nesting season on the day of recess) (Table 7.1). We visually examined a probability plot of the residuals for the global model to determine whether our hierarchical model adequately fit the data (Raudenbush and Bryk 2002). AGE and SEX variables were modeled using binary variables 0 and 1. SEASON and DOI were modeled using dummy variables to represent the three categories of early, middle, and late. We created 23 candidate models from the global prediction model that we perceived as being biologically relevant combinations of predictors. We calculated Akaike's Information Criterion values (Akaike 1973, Burnham and Anderson 2002; hereafter AIC), with the adjustment for small sample size (AIC_c) (Burnham and Anderson, 2002) for each model, and used AIC values in the model selection process to determine the combination of predictors that most influenced daily recess length. Additionally, we report estimates and 95% confidence intervals of recess duration from different predictor variable scenarios using our best-approximating model.

RESULTS

We viewed a total of 847 nest-days representing 20,328 hrs of incubation. From these, we described 885 nest recess events and 40 days in which no recess was observed, for a total of 925 daily recess observations (males = 451, females = 474). Apparent nesting success within our sample was 62% (73 of 117), and that of the entire study (excluding birds which abandoned due to research activities) was 60% (444 of 742). Mean clutch size among our sample nests (n = 118) was 12.6 eggs (95% CI: 12.1–13.2).

TABLE 7.1
Explanation of variables used to model daily nest recess length among Northern Bobwhites (Colinus virginianus) on three sites in southern Georgia and northern Florida, 1996–2006.

Variable	Explanation
CLUTCH	Refers to the clutch size (number of eggs) in the observed nest. If the value of a clutch is associated with its reproductive potential, a large clutch may be more valuable than a small clutch. This perceived value may affect investment and, consequently, nest recess frequency and duration.
SEX	A binary variable (1/0) describing whether the incubating bobwhite was male or female. Sex may impact parental investment and, consequently, patterns of nest recess and attendance.
AGE	A binary variable (1/0) describing the age (adult/juvenile) of the incubating bobwhite. Age of parent may be related to nesting experience and future reproductive potential, and may influence incubation behaviors including nest recess and attendance patterns.
POI	Refers to the period of incubation (early, middle, late) at the time of the nest recess. We classified early incubation as days 1–8, middle as days 9–16, and late as days 17–24. Stage of incubation is a direct reflection of investment and may influence recess frequency and duration.
SEASON	Describes the point in the nesting season at the time of the nest recess. We classified early season as May–June, middle as July, and late as August–September. Nesting season progression may be related to the number of nests attempted by an individual, body condition, and time left to successfully reproduce. These factors, either alone or in combination, may impact recess frequency and duration.

TABLE 7.2

Daily incubation recesses taken by period in nesting season, timing during incubation stage, and male and female bobwhites on three sites in southern Georgia and northern Florida, 1999–2006.

Recesses	Early Season	Mid Season	Late Season	Early Incubation	Mid Incubation	Late Incubation	Male	Female
0	16	12	12	9	16	15	18	22
1	256	189	288	167	346	220	346	387
≥2	30	17	27	25	31	18	43	31
Total	302	218	327	201	393	253	407	440

(Number of nest-days spans the eight data columns.)

Temporal Distribution of Recess Events

We observed 36% (302 of 847) of our recess events occurring during the early nesting period (May–June). The middle (July) and late nesting periods (August–September) represented 26% (218 of 847) and 39% (327 of 847) of recesses, respectively (Table 7.2). Across incubation, 24% (201 of 847) of observed recess events occurred in early incubation (days 1−8). The middle (days 9−16) and late incubation periods (days 17−23) accounted for 46% (393 of 847) and 30% (253 of 847) of recesses, respectively (Table 7.2). The difficulty in locating bobwhite nests and waiting for an initial incubation break to install equipment reduced our observations at the transition between egg-laying and start of incubation. Additionally, depredation of nests constrained our late incubation observations, because many nests did not survive to the hatching stage.

Daily Recess Frequency and Start Time

A single daily recess event was most common on 87% (733 of 847) of days (sexes combined). Bobwhites engaged in two or more daily recesses on 9% (74 of 847) of days, and no recesses were observed on 5% (40 of 847) of days (Fig. 7.1). We observed >2 daily recesses on only four of 847 days. Thus, we combined these observations into a "two or more" daily recess category for analysis. Most recesses were taken during the afternoon by both sexes. Males (median start time = 14:00 EST) consistently initiated recess earlier in the day than females (median start time = 15:00) (Fig. 7.2).
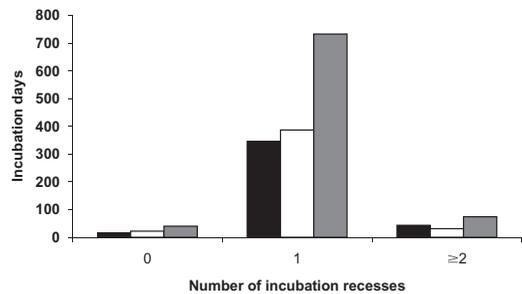

Figure 7.1. Number of daily incubation recesses taken by male (black), female (white), and combined (greygray) for bobwhites ($n = 118$ nests) on three sites in southern Georgia and northern Florida, 1999–2006.
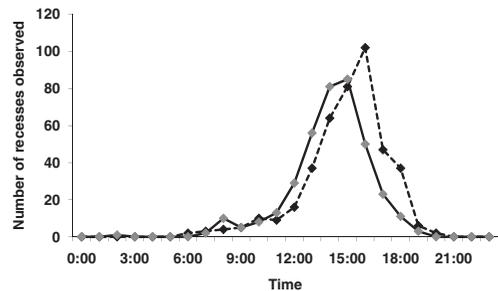

Figure 7.2. Start time of first daily nest recess by male (solid line; $n = 56$) and female (dashed line; $n = 62$) bobwhites on three sites in southern Georgia and northern Florida, 1999–2006. Time is EST.

Recess Duration

Mean total daily recess length was 182 min (95% CI: 98–264) for hatched nests and 224 min (95% CI: 140–308) for failed nests. Among failed nests, bobwhites engaged in two or more recesses on 14% (35 of 250) of days compared to 6% (32 of

TABLE 7.3

Predictors, number of parameters (K), deviance (Dev), ΔAIC$_c$, and Akaike weights (w$_i$), for the models containing any weight in the candidate model set used to explain daily nest recess length among bobwhites on three sites in southern Georgia and northern Florida, 1999–2006.

Model	K	Dev	ΔAIC$_c$	w_i
CLUTCH + SEASONMID + SEASONLATE + POIMID + POILATE	8	8,626.83	0.000	0.6918
CLUTCH + SEX + AGE + POIMID + POILATE + SEASONMID + SEASONLATE (Global)	10	8,624.35	1.623	0.3072
CLUTCH + SEX + SEASONMID + SEASONLATE	7	8,644.42	15.547	0.0003
CLUTCH + SEASONMID + SEASONLATE	6	8,647.11	16.197	0.0002
CLUTCH + POIMID + POILATE	6	8,647.83	16.920	0.00015
CLUTCH + SEX + AGE + SEASONMID + SEASONLATE	8	8,644.25	17.419	0.0001
CLUTCH + SEX + POIMID + POILATE	7	8,646.36	17.481	0.0001
CLUTCH + AGE + POIMID + POILATE	7	8,647.29	18.419	0.00007
AGE + POIMID + POILATE + SEX + CLUTCH	8	8,645.93	19.104	0.00005

533) of days for hatched nests. There was no difference in total daily recess length between males (204 min, 95% CI: 108–300) and females (186 min, 95% CI: 90–282), nor among birds that took one recess/d (201 min, 95% CI: 109–293) and birds that took two or more recesses/d (223 min, 95% CI: 129–317). Recess events on rainy days were 188 min (95% CI: 82–293) in duration, and those taken on clear days averaged 207 min (95% CI: 111–303).

Mixed Model Analysis and Model Selection for Recess Length

Visual examination of the residual probability plot for the residuals of the global model indicated the fit of the hierarchical models was adequate. Of the 23 models examined, nine had some AIC weight (Table 7.3). The best-fitting model contained CLUTCH + SEASONMID + SEASONLATE + POIMID + POILATE (Akaike weight = 0.692; Table 7.3). The next most likely model was our global model (CLUTCH + SEX + AGE + POIMID + POILATE + SEASONMID + SEASONLATE; Akaike weight = 0.307) (Table 7.3).

Two models contained 95% of the total AIC weight: the global model and a subset of that model (Table 7.3). However, since the best model is a subset of the second-best model, we focused our attention on the simplest explanation. From this model (Table 7.4), we estimated recess duration with 95% confidence intervals based upon

different combinations of POI, SEASON, and CLUTCH. We held clutch size constant as the average of 12.6 eggs (SE = 0.32) in all scenarios. Recess duration increased between early and mid-season, but duration declined slightly from middle to late season for all periods of incubation (Fig. 7.3). Slight decreases in recess duration were observed as period of incubation progressed across all seasons (Fig. 7.3). In the simplest model, clutch size, sex of parent, and age of parent did not affect recess length (Table 7.4).
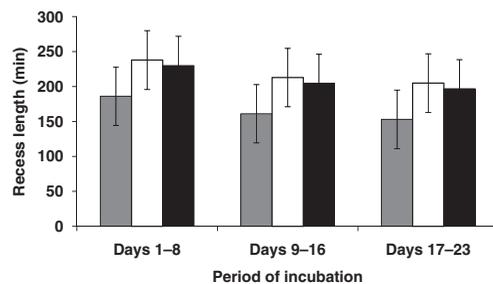

Figure 7.3. Predicted relationship between period of incubation (POI) and nesting season progression (SEASON; early: grey gray bars, middle: white bars, and late: black bars) with 95% CI on daily nest recess length among bobwhites on three sites in southern Georgia and northern Florida, 1999–2006. Data values reflect the mean fixed effect averaged across the best-fitting confidence set model that included POIMID, POILATE, SEASONMID, and SEASONLATE. The covariate CLUTCH was held constant at a mean of 12.6 eggs.

TABLE 7.4

Estimate, standard error, 95% confidence interval, and P-value for parameters included within the top model from the candidate model set used to explain daily nest recess length among bobwhites on three sites in southern Georgia and northern Florida, 1999–2006.

			95% CI		
Parameter	Estimate	SE	Lower	Upper	*P*
CLUTCH + SEASON + POI					
Intercept	164.490	32.324	100.150	228.830	<0.001
CLUTCH	1.715	2.299	−2.801	6.231	0.46
SEASON-MID	51.795	13.174	25.915	77.676	<0.001
SEASON-LATE	43.762	12.444	19.315	68.208	<0.001
POI-MID	−25.052	9.147	−43.022	−7.082	0.006
POI-LATE	−33.039	10.805	−54.266	−11.812	0.002

DISCUSSION

We observed variation both within and between bobwhites relative to recess frequency and length. Variation in daily recess patterns has been observed in prior studies on bobwhites (Stoddard 1931, Guthery et al. 2005), as well as in waterfowl and shorebirds (MacCluskie and Sedinger 1999, Cresswell et al. 2004, Gloutney et al. 2004, Lorenz 2005). Factors most influencing recess characteristics in our study were temporal in nature. We found nest recesses became shorter over time as the clutch progressed through incubation. Incubation recesses became longer toward the end of the nesting season when compared to early season nests. This has also been reported in waterfowl, suggesting that birds have greater energy requirements later in the season, possibly due to renesting (Gatti 1983). However, studies on other waterfowl have demonstrated contradictory results, which may be related to microclimate conditions in northern ecosystems (Loos 1999).

Recess Frequency and Start Time

Regardless of sex, most bobwhites engaged in one recess event per day; this is similar to Stoddard (1931), who noted bobwhites most frequently took one recess per day in the same region as our study. We found that two recesses were occasionally taken, and less frequently no recesses were observed. Because bobwhites are cryptic and nest on the ground in typically dense vegetation, our observations of days on which no recesses were taken may be an overestimate. It is possible that some recess events on these days were missed due to the parent bird leaving or approaching the nest from a different direction out of camera view. However, careful observation of video combined with the fact that the bird would have to both exit and reenter the nest unobserved should have minimized this bias.

Although the total amount of time spent in recess was not different between the sexes, males appeared to initiate recess earlier in the day than females. The reason for this is unclear, but to our knowledge this tendency has not previously been noted in the literature. Regardless of sex, most recesses were taken in mid to late afternoon. This is contrary to video observations of Greater Sage-Grouse (*Centrocercus urophasianus*), which revealed a bimodal distribution of recess periods, with peaks occurring around sunrise and sunset (Coates and Delehanty 2008). This pattern was attributed to anti-predator behavior to avoid diurnal corvids. Interestingly, in our study area the afternoon foraging trips coincide with the time of day that most predators were less active and during which we observed the fewest nest depredations (Burnam 2008). Furthermore, afternoon ambient temperatures in our study region are similar to the 30°C temperature average of bobwhite nest contents observed by Guthery et al. (2005). Therefore, foraging during this time may

have less impact on egg development and require less energy to reheat the egg. Nest attendance in Wild Turkeys (*Meleagris gallopavo*) has also been suggested to be temperature-influenced. Spohr (2001) found Wild Turkey hens in Connecticut recessed most frequently when temperatures and solar radiation were the highest. In Florida, a climate similar to our study area, Wild Turkeys were most likely to remain on the nest during peak temperatures and to recess during declining temperatures (Williams and Austin 1988). In Georgia, Burkhart (2004) found that shading by tall forbs significantly reduced overheating of ground habitats. Our study areas had well-developed annual and perennial forbs at ground level along with low-density pines, which provided shading during all parts of the day. This vegetative arrangement and resulting nest microclimate may further impact recess patterns when compared with adjacent areas comprised of different vegetative structure (Ar and Sidis 2002).

Recess Duration

Although the confidence intervals for daily recess length of successful and unsuccessful nests overlapped, likely due to a great deal of variation among birds, the biological ramifications of potential differences in daily recess length merit consideration. We note that mean daily recess lengths for birds attending failed nests averaged 42 min longer per day than recess lengths of birds attending successful nests. On average, when extrapolated across the entire 23-d incubation period, a parent at a successful nest was present at the nest for approximately 16 more hours of incubation than a parent at a failed nest. Because higher rates of attentiveness may influence hatching success and lower rates may expose eggs to temperature stress and predation (Yorio and Boersma 1994), this variation in daily attendance represents a great investment differential that may affect nest success. We also have observed that incubating adults were less likely to fight off swarms of ants when the ants invaded the nest during incubation breaks (Burnam 2008).

In our study, we found bobwhites spent less time in recess (thus, more time on the nest) in middle and late incubation compared to early incubation. An increase in investment throughout incubation has previously been noted in bobwhites, especially during late incubation, when

bobwhites may be reluctant to abandon a nest (Rosene 1969). A reduction in recess length as the clutch ages has also been shown in ground-nesting passerines (Weathers and Sullivan 1989) and supports the theory that a clutch increases in value with age (Barash 1975, Rytkonen et al. 1995). This increasing value and the energetic cost already invested in the nest result in greater attentiveness as hatching approaches. It also may represent an increasing vulnerability of the developing eggs to temperature changes (Romanoff and Romanoff 1949), which may require the incubating bobwhite to be more attentive to the nest.

The influence of hormones, particularly prolactin and testosterone, on nest recess and attendance has not been evaluated in bobwhites. However, numerous studies with waterfowl and passerine species indicate the importance of prolactin in influencing incubation behavior and parental investment (Goldsmith 1982, Hall 1987, Van Roo et al. 2003, Jonsson et al. 2006). Prolactin level is likely affected by tactile stimulation of the brood patch, visual, or thermal stimuli (Hall 1987), and has been shown to increase as incubation progresses (Jonsson et al. 2006). Conversely, prolactin levels have been shown to decrease after hatching in precocial species (Skutch 1976) or following clutch removal in waterfowl (Hall 1987). Given the relationship of prolactin levels to nest attentiveness in other similar species, it is possible that our observed increase in attendance as incubation progresses is influenced at least in part by similar hormonal cycles; however, future research should focus attention on hormone profiles to confirm these mechanisms in bobwhites and gain insight into the factors influencing hormonal changes throughout the incubation process.

We observed an overall increase in recess length across the middle and late nesting seasons relative to the early part of the season. Bobwhites are persistent renesters and may nest several times each season (Stoddard 1931, Stanford 1972). Nesting begins as early as April, and nest building, egg-laying, and incubation are energetically expensive endeavors that may affect a bobwhite's physical condition and resulting nest investment. As the nesting season progresses (e.g., August), an incubating bobwhite may have attempted several nests and possibly has depleted its physical reserves to the point that it must invest less in the current nest than it would have in a previous one.

If the prior nest was depredated well into incubation, the bird's physical decline may be even more pronounced following the rigors of extended attendance. In a nest attendance study on Ring-necked Pheasants (*Phasianus colchicus*), Persson and Göransson (1999) found that nest attendance and body condition at the start of incubation were positively correlated; as condition declined, so did attendance. Additionally, they found a negative relationship between attendance and number of breeding attempts (Persson and Göransson 1999). Essentially, if the demands of incubation and repeated nest attempts have depleted a bobwhite's physical reserves, the bird may be forced to spend more time foraging away from the nest in order to meet daily energetic requirements. Although birds in higher-quality habitat may enter the season in better physical condition, this scenario is exacerbated by vegetative and weather conditions in late summer. Most soft mast species are no longer producing, temperatures are hotter, and heavy thunderstorms with flooding may be more frequent. Therefore, a late-season bird in declining physical condition may need to spend more time foraging to achieve the same food intake and energetic benefits as the same bird earlier in the season. This seasonal stress is likely mitigated in better habitats, such as our study areas, and suggests the importance of quality habitat in bobwhite management.

Among the Galliformes, other than a few anecdotal observations, assessment of incubation behavior is rare. Although a few studies involved direct observation (e.g., Sande et al. 2001), studies typically use temperature changes in the nest to determine when females were absent (Persson and Göransson 1999). These technologies have substantial limitations relative to potential problems with indirect approaches, such as decisions about when an incubating bird leaves the nest based on temperature changes (Carroll 1990). Moreover, in hot climates temperature differentials may be in both directions from optimal incubation temperatures (Guthery 2000), making researcher decisions much more arbitrary. Though there are limitations with any technology (Ellis-Felege and Carroll, chapter 3, this volume), our study and that of Coates and Delehanty (2008) using video technology have improved the quality of incubation behavior data that can be obtained from the cryptic nests of Galliformes and have provided insights into Galliform ecology.

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