# USING CONTINUOUS VIDEO TO MONITOR PATTERNS OF NEST DEFENSE AND INCUBATION BEHAVIOR IN NORTHERN BOBWHITES (*COLINUS VIRGINIANUS)*

by

JONATHAN S. BURNAM

(Under the Direction of Dr. John P. Carroll)

## ABSTRACT

The incubation rhythms and nest defense patterns of attending northern bobwhites (*Colinus virginianus*; hereafter bobwhite) are poorly understood, largely due to a historical inability to directly monitor nests. Using continuous-recording, near-infrared cameras, we monitored incubation among bobwhites (118 nests randomly selected from a sample of 790 video-monitored nests), and viewed all nest depredations (n=241) to evaluate the parental, daily, and seasonal correlates that most contribute to patterns of nest recess, attendance, and nest defense in the bobwhite. We found that nest recess length decreased with clutch age and increased as the nesting season progressed. Predator species was the most influential factor in determining nest defense, and there was little difference between male and female bobwhites in nest attendance or defense patterns.

INDEX WORDS: northern bobwhite, nest attendance, nest defense, parental investment, nest behavior

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# DEDICATION

I would like to dedicate this thesis to my son, Levi.  It is my hope that we spend many April mornings standing together under a blooming dogwood waiting on that first early gobble.  I look forward to sharing with you a swim in the river in July, rising trout, bedding bream, baseball games, wood ducks squealing in a winter beaver pond, and the soft crunch of deer hooves in autumn's dry leaves.  Here's to the camaraderie of many evenings by a bright campfire while the songfeast tells the tale of the day.

It is my greatest hope however, that you find a deep love and respect for all things natural and wild, and that the simple things in life please you as much as they do your old man.  May you enjoy many sunny days afield.  I love you.

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To my parents Don and Beth Burnam, thank you for instilling within me the importance of education and hard work, and for allowing me free childhood reign through the woods and swamps of north Florida and south Georgia. Allowing me to grow up in the rural flatwoods is a gift for which I'm eternally grateful. To my grandfather Bill Gainey, who always encouraged a

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I love you to the moon and back.
-JB
Late spring, 2008

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# CHAPTER 1

# INTRODUCTION, LITERATURE REVIEW, AND STUDY OVERVIEW

## INTRODUCTION

Northern bobwhite (*Colinus virginianus*; hereafter bobwhite) populations in the southeastern U.S.A. have declined by 70-90% since the 1960's (Church et al. 1993, Brennan 1999). Several factors have been suggested as contributing to this decline, including changing land-use patterns, habitat loss (Brennan 1991), elimination of fire in pine forest ecosystems, and avian and mammalian predation (Burger et al. 1995, Yarrow and Yarrow 1999, Rollins and Carroll 2001). Although changes in land-use patterns are considered a major factor in bobwhite population declines on a regional scale, predation is often considered an important source of mortality and nest loss on a local scale (Errington and Stoddard 1938, Newton 1998, Rollins and Carroll 2001).

As a result of this decline, a great deal of research has been directed toward understanding bobwhite ecology. Consequently, bobwhites are one of the most studied species in North America (Guthery 1997, Williams et. al 2004). However, relatively little research has been conducted on the behavioral ecology of nesting bobwhites. Still fewer studies have used direct observation as a means for gathering behavioral data, primarily because a method for continuous, direct nest monitoring was unavailable. Bobwhites are cryptic, ground-nesting birds with nests that are widely dispersed across space and time. As in other birds, this spatial and temporal dispersion further complicates the task of observing and quantifying nest behavior (Brown et al. 1998).

During 1999-2006, continuous-recording, miniature video cameras were set up at 790 bobwhite nests on study sites in southern Georgia and northern Florida. We viewed a sample of these videos to quantify parental investment behaviors by directly observing incubation rhythms and patterns of nest defense among male and female bobwhites. We assessed these behaviors relative to predator species, and daily and seasonal correlates. Additionally, we investigated the relationship between nest-recess length and hatch rate, the difference between recess length among male and female incubating bobwhites, recess start time and the impact of season and clutch age on recess length and nest attendance.

Although bobwhite incubation behaviors are poorly understood, they likely have a great impact on annual recruitment. As a result, there is a need for greater understanding of bobwhite incubation and nest-defense patterns, and the factors that regulate them. Ultimately, a thorough characterization of the parental investment and incubation characteristics of the northern bobwhite will enable us to further understand this critical component of bobwhite ecology.

## BOBWHITE NESTING ECOLOGY

The northern bobwhite is a member of the Order Galliformes, and is widely distributed throughout the central and eastern United States and into Mexico (Brennan 1999). Once thought to be monogamous, recent research indicates bobwhites have a complex mating system with elements of polygyny and forms of polygamy (Curtis et al. 1993, Faircloth 2008). In the Southeast, pair formation begins in March and April, and as early as February when warm weather predominates (Stoddard 1931). Pair bonds may last from 2 weeks to several months (Faircloth 2008). The formation and disintegration of pair bonds appears based on the fate of nests and on subsequent breeding opportunities (Brennan 1999). Both sexes build the nest, which takes approximately 5 days to complete (Rosene 1969). The typical nest is comprised of grasses and pine needles and located on the ground immediately adjacent to protective cover, such as broomsedge and bluestem (*Andropogon spp.*) clumps, wiregrass (*Aristida spp*.) and herbaceous weeds. Most nests display some form of overhead structure (Brennan 1999) which serves to camouflage the nest and incubating parent as well as provide protection from avian predation.

The bobwhite hen lays slightly <1 egg per day, and the average clutch size is 12 – 15 subpyriform eggs. Egg laying is completed in approximately 18 days from the laying of the first egg (Rosene 1969). The number of eggs per clutch may decrease as the nesting season progresses, from an average of 16 eggs in May to 10 eggs in August, independent of nesting attempt (Cox et al. 2005). Incubation does not begin until after the last egg is deposited in the nest (Stoddard 1931). This delayed incubation may help facilitate synchronous hatching, which is an important attribute for a precocial, ground nesting bird species like the bobwhite.

Rollins and Carroll (2001) calculated a weighted success rate of 28% for bobwhite nests over a wide range of reported studies of nesting. Thus, bobwhites are persistent renesters, with up to 40% of females laying multiple clutches throughout the nesting season (Burger et al. 1995). Bobwhites are primarily uniparental incubators, with nests incubated by a single parent of either sex. Although most females will incubate a nest over the course of the nesting season, at least 25% of nests may be incubated by males (Stoddard 1931, Burger et al. 1995). During incubation, the non-attending parent avoids the nest site, but will quickly assume incubation duties in the event of mortality to the attending parent. The incubating parent will leave the nest

1-3 times a day to engage in foraging recess. Recess events vary in length but are usually conducted in the afternoon (Stoddard 1931).

Pipping begins 2 days prior to hatching and indicates pulmonary respiration in the chick (Vince 1964). Hatching begins approximately 23 days after the initiation of incubation. Most eggs hatch within a few hours of the first and the adult and brood leave the nest bowl together shortly after hatching is complete (Brennan 1999). A female may renest in 1-2 days after hatching if her mate assumes responsibility for the brood (Curtis et al. 1993).

## AVIAN PARENTAL INVESTMENT

Parental investment and incubation behaviors, in particular nest recess and attendance, are aspects of bobwhite ecology that merit further study. Parental investment is 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 (Trivers 1972). Parental investment theory states that parents base investment decisions on expected future benefits and not on the cost of past investment. However, if reproduction is associated with cost, then expected benefits and past investment are confounded (Sargent and Gross 1984). Parents must then assess the value of the clutch relative to future reproduction, and maximize lifetime reproductive opportunities (Williams' Principle).

A multitude of factors may affect investment behaviors, including reproductive ecology, sex and age of parent, habitat quality, clutch age, and whether it is early or late in the nesting season (Trivers 1972, Moller 1991, Rauter and Reyer 1997). As a key component in an individual's fitness, parental investment is of interest from both management and evolutionary perspectives. The amount and type of parental care among bird species varies along the altricial-precocial spectrum, with most species exhibiting some degree of biparental care (Kendeigh 1952, Skutch 1957, Starck and Ricklefs 1998, Tremont and Ford 2000). However, uniparental incubation is most common in species with precocial young (e.g. bobwhites). Among these species, the non-incubating parent may be involved with territory defense or may pursue additional mating opportunities.

Gender of the incubating parent is another factor that may influence investment in the clutch. In theory, females are more likely to remain with the nest due to higher gametic costs for females compared to males (Trivers 1972). Conversely, males may be less certain of paternity. Thus, they may spend more time pursuing extra-pair copulations and less time investing in the nest, particularly in populations with a female bias (Westneat and Sherman 1993, Sheldon et al. 1997, Burley and Calkins 1999). The sex ratio in the population may impact current investment by affecting additional reproductive possibilities. Essentially, if the sex ratio is biased, the overrepresented sex may invest more in the clutch if the underrepresented sex invests less (Burley and Calkins 1999).

Habitat quality may impact parental investment in the clutch by impacting body condition and the daily energy expenditure necessary to meet metabolic requirements. In general, birds are capable of storing fats and proteins for later utilization (Ankney and MacInnes 1978, Hohman 1986). Afton and Paulus (1992) found that larger waterfowl species with greater body reserves spent less time foraging than did smaller species, presumably due to greater storage of endogenous reserves. This suggests that birds (especially income breeders such as bobwhites) nesting in higher quality habitat may invest less time in foraging activities due to better body condition and more readily available food.

Stage of incubation (or clutch age) likely affects the parent’s investment in the clutch. Rosene (1969) noted that the incubating bobwhite becomes increasingly less likely to abandon the nest as incubation progresses. If the value of a clutch is directly related to the cost of replacement (Dawkins and Carlisle 1976), then older clutches require less future investment and would therefore warrant more current investment (Lifjeld and Slagsvold 1990).

Finally, parental investment in the clutch may be affected by the stage of the nesting season. A bird with a nest destroyed in May has a great deal more time to renest than a bird with a nest depredated in August. As a result, the August parent may be more inclined to invest heavily in the clutch as a "last-ditch" effort to successfully raise a brood. Opportunities for extra-pair copulations are also higher early in the breeding season, therefore more time may be spent pursuing additional mating opportunities (Moller 1991).

Conversely, it is also possible that nests initiated later in the season may receive less parental attention than their early season counterparts. Incubation and egg-laying come at an energetic cost to the parent, causing a decline in the parent's body condition as the nesting season progresses (Tveraa et al. 1997, Hanssen et al. 2002). This would certainly seem true if the bird were attempting a 2nd or 3rd nest. This decline in physical condition may warrant more frequent foraging trips and lessen the likelihood of defensive behaviors.

## NEST ATTENDANCE IN BOBWHITES

Daily nest attendance and recess patterns assume an important role in bobwhite reproductive ecology. We define nest attendance as anytime during which the parent is incubating eggs in the nest. For our purposes, nest recess is anytime the parent is away from the nest bowl, and thus not actively involved in incubation.

The energetic costs of incubation are high (Monaghan and Nager 1997), and birds are likely constrained from attending more due to the depletion of energy reserve levels (Cresswell et al. 2004). Since 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 trade-off between meeting the metabolic needs of the parent, minimizing predation risk, and maintaining a suitable environment for the developing embryos (Afton 1980, Flint and Grand 1999). A parent bird's ability to balance daily energetic needs with embryo requirements is a continual struggle influenced by the 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. Gloutney et al. (2004) found that recess times among Ross's and lesser snow geese (*Chen rossii* and *Chen caerulescens,* respectively) varied widely by reproductive stage and food intake. Likewise, incubation initiation has been shown to vary among conspecifics with regards to individual body condition and egg size (Hanssen et al. 2002).

Among bobwhites, thermal conditions may impact attendance. Although there is little seasonal adjustment in bobwhite metabolism and insulation (Swanson et. al 1997), bobwhites may defend eggs more vigorously against hyperthermia than hypothermia (Guthery et al. 2005) possibly influencing recess length and ultimately recruitment.

## NEST DEFENSE IN BOBWHITES

Nearly all birds are subject to predation (Newton 1998). Nest predation, in particular, is an important factor affecting fitness and reproductive behavior for many bird species (Ricklefs 1969, Lind and Cresswell 2005). As a result, any bird whose behavioral characteristics facilitate the avoidance or deterrence of nest predation will be more likely to produce offspring. Nest predation risk is frequently a composite of several factors, but risk may be limited through either direct defense or through predation risk compensation (Lind and Cresswell 2005). Predation risk compensation occurs when an infrequently-expressed anti-predation behavior is compensated for by another, more strongly displayed anti-predation behavior. For example, an individual bird may be less likely to physically defend its clutch, but may compensate by constructing a cryptic nest in an area that is infrequently used by predators.

By comparison, nest defense is defined as any activity by the parent that decreases the likelihood of damage to the nest or its contents while simultaneously increasing parental risk (Montgomerie and Weatherhead 1988). When a nest depredation occurs, the likelihood of defense is influenced by the value of the offspring relative to the parent, and the parent's ability to produce more offspring in the future (Brunton 1986). Nest defense is then a direct reflection of parental investment and is thus affected by many of the same factors that influence other aspects of nesting and incubation.

Although nest defense studies have been conducted on species with precocial young (Sandercock 1994, Mallory et al. 1998), nest defense behaviors have been studied primarily in the context of parental investment and mostly in passerine species with altricial young (Knight and Temple 1988, Whittam and Leonard 2000). These studies primarily used humans or model predators to gauge the parents' response in a direct, controlled manner (Knight and Temple 1986, Hatch 1997). Natural predation events among bobwhites and other Galliformes are rarely observed and difficult to study directly because they are widely dispersed in space and time (Pettingill 1976, Brown et al. 1998). Until recently, indirect observation was the primary method by which depredation data were collected on bobwhite nests. Staller et al. (2005) used miniature video cameras with recorders set up at nests to directly identify predators and correlate diagnostic sign at the nest with the predator responsible for the depredation. This method is also useful for interpreting a variety of other nesting behaviors, including nest defense.

Parental characteristics such as renesting potential (Barash 1975, Ghalambor and Martin 2000), age (Pugesek 1983), and breeding experience (Montgomerie and Weatherhead 1988) may affect the likelihood of defense. Clutch age may also impact defense because offspring become increasingly valuable with age, and become more costly to replace (Ricklefs 1973). Likewise, defense should increase as incubation progresses and as the end of nesting season approaches (Biermann and Robertson 1981).

A bird’s response to a potential nest depredation may be predator-specific, and may vary according to the danger the predator poses to the nest and the parent (Gochfeld 1984). That perceived danger is likely a direct reflection of the mobility and armament of the predator (Montgomery and Weatherhead 1988). Thus, nest predators that pose little risk to the parent may more likely be defended against than a predator that poses a risk to both parent and nest. From an evolutionary perspective, it would be maladaptive to die defending a nest when it could be abandoned and soon replaced with another.

## STUDY OVERVIEW

The objective of this study was to examine parental investment behaviors and patterns of nest defense among nesting bobwhites. Videotapes of bobwhite nests collected from 3 sites during 1999 to 2006 (n=790) were viewed to collect data for analysis. Because of the difficulty in locating nests before the end of egg laying and the beginning of incubation, all observed nests were actively incubated. We gathered nest recess data by randomly sampling birds (n=118 nests) across the sites from each year of the study. We viewed all available depredation events (n=241 events) to evaluate depredation characteristics and nest defense behaviors. Logistic regression was used to model the probability of nest defense based on several potential predictor variables. Mixed models were used to examine nest attendance of bobwhites. Akaike's Information Criterion (Akaike 1973, Burnham and Anderson 2002) was used in the model selection process for both nest defense and attendance to determine the combination of predictors that best explained the data. We also compiled basic descriptive statistics using proportions (%) and means with 95% confidence intervals (95% CI) and standard error (SE) to further explain and compare our findings.

By analyzing nest recordings made from 1999 to 2006, we investigated the following:

1. How does nest defense differ between incubating male and female bobwhites?
2. Does nest defense vary with different predators, nesting period, clutch size, or incubation investment?
3. What is the relationship between nest recess length and hatch rate? Between male and female recess length?
4. Does time spent in recess vary with nesting period, incubation investment, clutch size, and weather?

This thesis is divided into 4 chapters, with each chapter written so that it may stand alone in the context of the thesis as a whole. This chapter provides an overview of the study, general parental investment theory, bobwhite nesting ecology, and the interaction of investment theory on incubation and nest defense. Chapter II addresses bobwhite nest defense behaviors and the factors contributing to nest defense. We also quantify characteristics of nest depredations with regards to each different species of predator. In Chapter III, we investigate patterns of nest recess and attendance, and evaluate the impact of parental characteristics and temporal correlates on recess length and hatching success. Finally, Chapter IV is a summary of the study, with conclusions and topics to be addressed by future research. Hopefully, this research will serve as a framework for future investigations into the behavioral ecology of ground nesting upland birds.

## LITERATURE CITED

Afton, A.D. 1980. Factors affecting incubation rhythms of northern shovelers. Condor 82:132 137.

Afton, A.D. and S.L. Paulus. 1992. Incubation and brood care. Pages 62-108 in B.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu, eds. Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, MN. 635pp.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* Proceedings of Second International Symposium on Information Theory. B.N Petrov and F. Csaki, editors. Akademiai Kiado, Budapest, Hungary.

Ankney, C.D., and C.D. MacInnnes. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459-471.

Barash, D.P. 1975. Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. Wilson Bulletin 87:367-373.

Biermann, G.C., and R.J. Robertson. 1981. An increase in parental investment during the breeding season. Animal Behaviour 29:487-489.

Brennan, L.A. 1991. How can we reverse the northern bobwhite population decline? Wildlife Society Bulletin 19:544-545.

___________. 1999. Northern bobwhite *Colinus virginianus.* In the Birds of North America No. 397. A. Poole and F. Gill, editors. The Birds of North America, Inc., Philadelphia, PA, USA.

Brown, K.P., H. Moller, J. Innes, and P. Jansen. 1998. Identifying predators at nests of small birds in a New Zealand forest. Ibis 140:272-279.

Brunton, D.H. 1986. Fatal antipredator behavior of a killdeer. Wilson Bulletin 98:605-607.

Bryan, S. and D.M. Bryant. 1999. Heating nest boxes reveals an energetic constraint on incubation behavior in great tits, *Parus major*. Proc R Soc Lond B 266:157-162.

Burger, L.W., M.R. Ryan, T.V. Dailey, and E.W. Kurzejeski. 1995. Reproductive strategies, success, and mating strategies of northern bobwhites in Missouri. Journal of Wildlife Management 59:417-426.

Burley, N.T., and J.D. Calkins. 1999. Sex ratios and sexual selection in socially monogamous zebra finches. Behavioral Ecology 10:626-635.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and inference: an information-theoretic approach. Springer-Verlag, New York, NY.

Church, K.E., J.R. Sauer, and S. Droege. 1993. Population trends of quails in North America. Proceedings of the National Quail Symposium 3:44-54.

Cox, S.A., F.S. Guthery, J.L. Lusk, A.D. Peoples, S.J. Demaso, and M. Sams. 2005. Reproduction by northern bobwhites in western Oklahoma. Journal of Wildlife Management 69(1):133-139.

Cresswell, W., S. Holt, J.M. Reid, D.P. Whitfield, R.J. Mellanby, D. Norton, and S. Waldron. 2004. The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. Behavioral Ecology 15:498-507.

Curtis, P.D., B.S. Mueller, P.D Doerr, C.F. Robinette, and T. Devos. 1993. Potential polygamous breeding behavior in the northern bobwhite. Proceedings of the National Bobwhite Quail Symposium 3:55-63.

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

Errington, P.L., and H.L. Stoddard. 1938. Modifications in predation theory suggested by ecological studies of the bobwhite quail. Transactions of the North American Wildlife Conference. 3:736-740.

Faircloth, B.C. 2008. Social and reproductive systems in Northern Bobwhite (*Colinus virgininaus*); a non-migratory, avian species bearing precocial young: an integrative study. PhD Dissertation, University of Georgia, Athens.

Flint, P.L., and J.B. Grand. 1999. Incubation behavior of spectacled eiders on the Yukon-Kuskokwim Delta, Alaska. Condor 101:413-416.

Ghalambor, C.K. and T.E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Animal Behaviour 60:263-267.

Gloutney, M.L., R.T. Alisauskas, A.D. Afton, and S.M. Slattery. 2004. Foraging time and dietary intake by breeding Ross's and lesser snow geese. Oecologia 127:78-86.

Gochfeld, M. 1984. Antipredator behavior: aggressive and distraction displays of shorebirds. Pp. 289-377 *in* J. Burger and B.L. Olla, Editors. Shorebird Breeding Biology and Populations. Plenum Press, New York.

Guthery, F.S. 1997. A philosophy of habitat management for northern bobwhites. Journal of Wildlife Management 61:291-301.

Guthery, F.S., A.R. Rybak, S.D. Fuhlendorf, T.L. Hiller, and S.G. Smith. 2005. Aspects of the thermal ecology of bobwhites in north Texas. Wildlife Monographs 159:1–36.

Hanssen, S.A., H. Engebretsen, K.E. Erikstad. 2002. Incubation start and egg size in relation to body reserves in the common eider. Behavioral Ecology and Sociobiology 52:282-288.

Hatch, M.I. 1997. Variation in song sparrow nest defense: Individual consistency and relationship to nest success. Condor 99:282-289.

Hohman, W.L. 1986. Incubation rhythms of Ring-necked Ducks. Condor 88:290-296.

Kendeigh, S.C. 1952. Parental care and its evolution in birds. Illinois Biological Monographs. 22:1-358.

Knight, R.L., and S.A. Temple. 1986. Why does intensity of avian defense increase during the nesting cycle? Auk 103:318-327.

________________________. 1988. Nest-defense behavior in the red-winged blackbird. Condor 90:193-200.

Lifjeld, J.T., and T. Slagsvold. 1990. Manipulations of male parental investment in polygamous pied flycatchers, *Ficedula hypoleuca*. Behavioral Ecology 1:48-54.

Lind, J. and W. Cresswell. 2005. Determining the fitness consequences of antipredation behavior. Behavioral Ecology 16:945-956.

Lorenz, N.F. 2005. Environmental factors influencing incubation constancy and recess frequency in gadwall (*Anas strepera*) in the prairie pothole region of North Dakota. M.S. Thesis, Louisiana State University, Baton Rouge.

Mallory, M.L., D.K. McNicol, and R.A. Walton. 1998. Risk-taking by incubating common goldeneyes and hooded mergansers. 100:694-701.

Moller. A.P. 1991. Double broodedness and mixed reproductive strategies by female swallows. Animal Behavior 42:671-679.

Monaghan, P. and R.G. Nager. 1997. Why don't birds lay more eggs? Trends in Ecology & Evolution 12:270-274.

Montgomerie, R.D. and P.J. Weatherhead. 1988. Risks and rewards of nest defence by parent birds. Quarterly Review of Biology 63:167-187

Newton, I. 1998. Population limitation in birds. Academic Press Limited, San Diego, CA, USA.

Pettingill, O.S., Jr. 1976. Observed acts of predation on birds in northern lower Michigan. Living Bird 15:33-41.

Pugesek, B.H. 1983. The relationship between parental age and reproductive effort in the California gull (*Larus californicus*). Behavioral Ecology and Sociobiology 13:161-171.

Rauter, C., and H. Reyer. 1997. Incubation pattern and foraging effort in the female water pipit *Anthus spinoletta*. Ibis 139:441-446.

Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. 9:1-48.

___________. 1973. Ecology. Chiron Press, New York.

Rollins, D., and J.P. Carroll. 2001. Impacts of predation on northern bobwhite and scaled quail. Wildlife Society Bulletin 29:39-51.

Rosene, W. 1969. The bobwhite quail: its life and management. Rutgers University Press, New Brunswick, New Jersey.

Sandercock, B.K. 1994. The effect of manipulated brood size on parental defence in a precocial bird, the willow ptarmigan. Journal of Avian Biology 25:281-286.

Sargent, R.C., M.R. Gross. 1985. Parental investment decision rules and the Concorde fallacy. Behavioral Ecology. 17:43-45.

Sheldon, B.C., K. Rasanen, and P.C. Dias. 1997. Certainty of paternity and paternal effort in the collared flycatcher. Behavioral Ecology 8:421-428.

Skutch A. F. 1957. The incubation patterns of birds. Ibis 99:69–93.

Staller, E.L., W.E. Palmer, J.P. Carroll, R.P. Thornton, and D.C. Sisson. 2005. Identifying predators at northern bobwhite nests. Journal of Wildlife Management 69:124-132.

Starck, J. M. and Ricklefs, R. E. 1998. Patterns of development: the altricial-precocial spectrum. Pp. 3-30 i*n* Avian Growth and Development. Oxford: Oxford University Press.

Stearns, S.C. 1992. The evolution of life histories. Oxford: Oxford University Press.

Stoddard, H.L. 1931. The bobwhite quail: its life history and management. Charles Scribner's Sons, New York, USA.

Swanson, D.L. and D.P. Weinacht. 1997. Seasonal effects on metabolism and thermoregulation in northern bobwhite. Condor 99:478-489.

Tremont. S. and H.A. Ford. 2000. Partitioning of parental care in the leaden flycatcher. Emu 100:1-11.

Trivers, R.L. 1972. Parental investment and sexual selection. Pp. 136-179 *in* B. Campbell, Editor. Sexual Selection and the Descent of Man. Chicago: Aldine.

Tveraa, T., S.H. Lorentsen, and B.E. Saether. 1997. Regulation of foraging trips and costs of incubation shifts in the Antarctic petrel (*Thalassoica antarctica*). Behavioral Ecology 8:465-469.

Vince, M.A. 1964. Social facilitation of hatching in the bobwhite quail. Animal Behaviour 12:531-534.

Westneat. D.F. and P.W. Sherman. 1993. Parentage and the evolution of parental behavior. Behavioral Ecology 4:66-77.

Whittam, R.M., and M.L. Leonard. 2000. Characteristics of predators and offspring influence nest defense by arctic and common terns. Condor 102:301-306.

Williams, C.K., F.S. Guthery, R.D. Applegate, and M.J. Peterson. 2004. The northern bobwhite decline: scaling our management for the twenty-first century. Wildlife Society Bulletin 32:861-869.

Yarrow, G.K., and D.T. Yarrow. 1999. Managing for bobwhite quail. Pp. 165-183 *in* Managing Wildlife. Sweet Water Press, Birmingham, AL, USA.

# CHAPTER 2

# MONITORING PATTERNS OF NEST DEFENSE AND DEPREDATION CHARACTERISTICS AT NORTHERN BOBWHITE NESTS[1]

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## INTRODUCTION

The northern bobwhite (*Colinus virginianus*; hereafter bobwhite) is a species in decline (Church et al. 1993, Brennan 1999). As a result of this decline, a great deal of research has been directed toward understanding bobwhite ecology. Consequently, bobwhites are one of the most-studied species in North America (Guthery 1997, Williams et. al 2004). However, relatively little research has been conducted on the behavioral ecology of nesting bobwhites, particularly with regards to patterns of nest defense.

Nearly all birds are subject to predation (Newton 1998). Nest predation, in particular, is an important factor affecting fitness and reproductive behavior for many bird species (Ricklefs 1969, Lind and Cresswell 2005). As a result, any bird whose behavioral characteristics facilitate the avoidance or deterrence of nest predation will be more likely to produce offspring. Nest predation risk is frequently a composite of several factors (Lind and Cresswell 2005) and may vary according to nest location, stage of the nesting season, and the predator context of the area among other factors.

By comparison, nest defense is defined as any activity by the parent that decreases the likelihood of damage to the nest or its contents while simultaneously increasing parental risk (Montgomerie and Weatherhead 1988). In contrast to the temporal and ecological factors listed above, nest defense is a direct, conscious engagement initiated by the incubating bird. When a potential nest depredation occurs, the likelihood of defense is influenced by the value of the offspring relative to the parent, and the parent’s ability to produce more offspring in the future (Brunton 1986). Nest defense is then a direct reflection of parental investment and is thus affected by many of the same factors that influence other aspects of nesting and incubation.

Parental characteristics, such as renesting behavior (Barash 1975, Ghalambor and Martin 2000), age (Pugesek 1983), and breeding experience (Montgomerie and Weatherhead 1988) may affect the likelihood of defense. Clutch age may also impact defense because offspring become increasingly valuable with age, and become more costly to replace (Ricklefs 1973). Likewise, defense should increase as incubation progresses and as the end of nesting season approaches (Biermann and Robertson 1981). A bird's response to a potential nest depredation may be predator-specific, and may vary according to the danger the predator poses to the nest and the parent (Gochfeld 1984). That perceived danger is likely a direct reflection of the mobility and armament of the predator (Montgomery and Weatherhead 1988). Thus, nest predators that pose little risk to the parent may more likely be defended against than a predator who poses a risk to both parent and nest. For persistent renesters, from an evolutionary perspective, it would be maladaptive for a parent to defend a nest when it could be abandoned and soon replaced with another.

Although nest defense studies have been conducted on species with precocial young (Sandercock 1994, Mallory et al. 1998), nest defense behaviors have been studied primarily in the context of parental investment and mostly in passerine species with altricial young (Knight and Temple 1988, Whittam and Leonard 2000). As in other birds, natural predation events among bobwhites and other Galliformes are rarely observed and difficult to study directly because they are widely dispersed in space and time with cryptic nests (Brown et al. 1998, Pettingill 1976). Until recently, indirect observation was the primary method by which depredation data were collected on bobwhite nests. Staller et al. (2005) used miniature video cameras with recorders set up at nests to directly identify predators and correlate diagnostic sign at the nest with the predator responsible for the depredation. This method is also useful for interpreting a variety of other nesting behaviors, including nest defense.

The northern bobwhite is a ground-nesting bird and is subject to high rates of nest predation. Rollins and Carroll (2001) reviewed bobwhite studies from across the U.S.A. and calculated a weighted nest success rate of 28%. Common bobwhite nest predators included, but were not limited to, raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginianus*), bobcat (*Felis rufus*), nine-banded armadillo (*Dasypus novemcinctus*), snakes (particularly *Elaphus sp.* and *Lampropeltis getulus*) and fire ants (*Solenopsis spp.*). Some of these predators are capable of killing the parent bird, whereas others are only a threat to the nest contents.

We directly observed bobwhite nest depredations in order to quantify patterns of nest defense and general depredation characteristics along a spectrum that includes predator species and a variety of daily and seasonal correlates. We predicted varying defensive response associated with predator species, nesting season progression, and investment in the clutch.

## METHODS

### Study Site

Our study area consisted of 3 sites. Tall Timbers Research Station, located in northern Florida, and Pebble Hill Plantation and Pinebloom Plantation are in southwestern Georgia. 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 (*Pinus palustris*) and shortleaf pine (*Pinus echinata*) also present in the uplands. 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 (Thornton 2003). Autumn covey counts estimate 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.

During 1999 - 2006, bobwhites were captured from January to April using baited "walk in" funnel traps (Smith et al. 1981). Captured bobwhites were classified by age and sex, and fitted with 6.5g pendant-style radio-transmitters (Staller et al. 2005). All procedures involved in trapping, handling, and banding captured birds followed the guidelines presented in the American Ornithologists' Union Report of Committee 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). Bobwhites were monitored on a daily basis and assumed to be nesting when in the same location for 2 consecutive days. Nests were then located using telemetry homing techniques (White and Garrott 1990).

### Camera System

We installed continuous-recording, near-infrared video cameras at bobwhite nests and monitored the birds throughout incubation. The video camera system was comprised of a N9C2 Fieldcam LRTV Microcam with a 3.7mm wide-angle lens and a 6-array LED at 950 nm (Furman Diversified, Inc.). Sunlight provided ample light for daytime recording, and nighttime recording was supported by an auxiliary 36-array LED infrared illumination system with a wavelength of 950 nm. Both components were supported on a camouflaged articulating arm attached to a wooden stake. A VHS time-lapse recorder that continuously recorded 20 frames per second was connected to the camera and illumination system. Since the recording rate was 1/3 normal speed, each 8 hour tape lasted 24 hours (Staller et al. 2005).

Cameras were installed 1.5 – 2 m from the nest bowl while the incubating parent was away. Modification of vegetation was minimized and the camera and components were camouflaged for minimum disturbance. Recorders and power supplies were linked by cable and situated approximately 30 m from the nest. Care was taken to prevent cables and cords from crossing likely predator travel routes such as firebreaks and roads (Staller et. al 2005). After installing the camera, the nest was monitored every 1-2 hours to ensure the bird returned to resume incubation. If the bird had not returned within 4-6 hours, the camera was adjusted and placed at an angle to the nest to further minimize disturbance to the incubating bird. A technician replaced tapes and batteries every 24 hours until nesting was complete or the nest was depredated. Tapes were labeled with the individual bird identification number for use in acquiring bird-specific information for data analysis.

### Data Collection

We selected nest videotapes representing 241 events that were indicated in the database as being depredations, either through direct observation or a reduction in a subsequent egg count as noted by a technician. Because of the difficulty in locating nests before the end of egg laying and the beginning of incubation, all observed nests were actively incubated. We viewed each depredation and recorded bird identification number, sex, age of the bird (adult/juvenile), site (plantation), date of depredation event, predator species, depredation start time and duration, period of incubation, nesting period, and clutch size. Depredation time was recorded as beginning when the bobwhite first flushed or initiated defensive action, and ended at the last camera view of the predator. We categorized period of incubation at the time of depredation as early (day 1-8), middle (day 9-16), and late (day 17-24) according to the reported incubation start date in the database. Likewise, nesting period was defined as early (May-June), middle (July), and late (August-September) according to the date of the depredation. For each depredation event, we noted if the bobwhite flushed and we estimated the distance (in 0.3 meter increments) from the predator to the nest at flushing. Although in some cases we could identify snakes at the species level (in most cases corn snake (*Elaphe guttata guttata*), gray rat snake (*Elaphe obsolete spiloides*), or eastern kingsnake (*Lampropeltis getula getula*), we chose to pool them into one "snake" category due to very little inter-specific variation in their depredation characteristics. Mammals and avian predators were recorded according to individual species.

For each depredation, we recorded if the incubating bobwhite engaged in any defensive behaviors against the nest predator. We defined defensive behavior as any voluntary physical or behavioral engagement by the parent against the predator. Thus, non-physical engagements such as posturing and pacing are included because they endanger the parent while attempting to protect the nest and its contents. Defensive behaviors were ultimately classified as direct attack, broken wing, posture (display), pecking, pacing, or a combination of these behaviors. We did not label any event as "defended" or "not defended" unless we could identify the bird either flushing/leaving the nest or engaging in defense.

### Data Analysis

We believed that the likelihood of defensive action could potentially be influenced by a suite of parental characteristics, predator demographics, and temporal conditions. Thus, we used logistic regression analysis to model the probability of nest defense based on several predictor variables. To avoid multicollinearity, we conducted Pearson correlations on all pairs of predictor variables to ensure no correlations had a value of $r^2 > 0.2$. We assessed goodness-of-fit by running a Hosmer-Lemeshow test where a fit is adequate if $P > 0.05$ (Hosmer and Lemeshow 1989).

Our global prediction model consisted of PRED (snake & ant species, mammals as baseline), SEX (sex of incubating parent), AGE (age of incubating parent), DOI (period of incubation at the time of depredation), and SEASON (stage of nesting season at the time of depredation) (Table 2.1). We created 31 candidate model sets from the global prediction model and used Akaike's Information Criterion (Akaike 1973, Burnham and Anderson 2002) in the model selection process to determine the combination of predictors that best explained the likelihood of defense. We then calculated AIC values with the adjustment for small sample size ($AIC_c$) (Burnham and Anderson, 2002) for each predictor model and herein report the 10 of 31 models containing 95% of the total candidate model-set weight. In addition to the analyses above, we compiled basic descriptive statistics using proportions and means ± 95% CI to further explain and compare our findings.

## RESULTS

From a total of 790 monitored nests we observed 241 depredation events occurring during 1999 - 2006. Depredated nests were incubated by 195 female bobwhites, 41 males, and 5 birds of undetermined sex. Predator species observed during events included, snakes (n=92), armadillo (n=33), opossum (n=31), raccoon (n=27), fire ants (n=22), bobcat (n=18), fox squirrel (*Sciurus niger*) (n=4), cotton rat (*Sigmodon hispidus*) (n=2), coyote (*Canis latrans*) (n=1), barred owl (*Strix varia*) (n=1), feral hog (*Sus scrofa*) (n=1), white-tailed deer (*Odocoileus virginianus)* (n=1), and 8 unknown predators. Unknown predators are likely snakes or ants, thus these species may be underrepresented.

Of these events, 107 (44%) occurred during the early nesting period (May-June), 66 (27%) occurred during the middle nesting period (July), and 68 (28%) took place in late nesting (August-September). Across period of incubation, 87 (37%) depredations occurred during early

Table 2.1. Explanation of variables used to predict the likelihood of nest defense among northern bobwhites (*Colinus virginianus*) on three plantations in southern Georgia and northern Florida, 1999-2006.

| **Variable** | **Explanation** |
|---|---|
| PRED | Refers to the snake/fire ant category of predators. Mammals were the additional classification and served as the baseline in the analysis. Predators were grouped in this manner to facilitate data separation and because as a group, mammals are often controlled in an effort to increase bobwhite populations. |
| SEX | A binary variable (1/0) describing whether the incubating bobwhite was male or female. Sex may impact parental investment and consequently, the likelihood of nest defense. |
| 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 the likelihood of nest defense. |
| DOI | Refers to the stage of incubation (early, middle, late) at the time of the nest depredation. 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 defense. The demographics of nest predators may also vary as incubation progresses. |
| SEASON | Describes the point in the nesting season at the time of the nest depredation. 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. The demographics of nest predators may also vary as the nesting season progresses. |

incubation (days 1-8), 88 (37%) took place in middle incubation (days 9-16), and 62 (26%) were observed during late incubation (days 17-24).

### Nest Defense

We observed 55 active defenses against nest predators. Bobwhites engaged in nest defense behaviors against snakes (n=25), nine-banded armadillos (n=16), fire ants (n=10), cotton rats (n=2), and squirrels (n=2). We observed no cases of nest defense against raccoons, opossums, bobcats, coyotes, white-tailed deer, feral hogs, or avian predators. In events involving this latter suite of predators, the parent bird invariably flushed or was killed and made no attempt to defend the nest. Mean clutch size of defended nests (13.1 eggs ± 0.9, 95% CI) and non-defended nests (12.8 eggs ± 0.7, 95% CI) did not differ.

With the exception of ants (which were primarily pecked), broken wing display and combinations of direct attack, broken wing, and posture were the primary defensive behaviors observed against every defended predator species. Distraction displays (broken wing, posture, pacing) were used alone 19 times (37%) and in conjunction with direct attack 20 times (38%), often after the initial attack failed to deter the predator (Figure 2.1). Direct attack alone was used 8 times (15%), most frequently when the bobwhite detected the predator before the animal reached the nest. If the defensive behaviors did not serve to discourage the predator, the attending bobwhite would often pace back and forth while the predator was raiding the nest. We observed this behavior at 17 (33%) depredations. This agitated pacing behavior did not occur at depredations by raccoons, opossums, and bobcats. In events involving these species, the bobwhite typically flushed immediately and returned hours later to inspect the nest contents before abandoning.

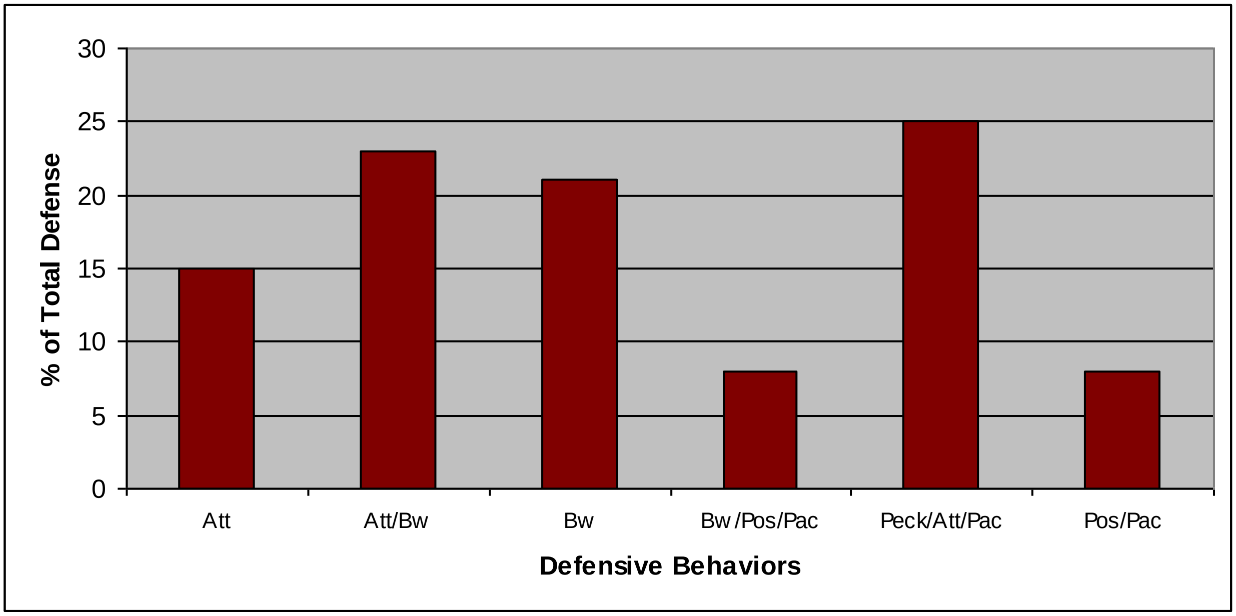

Figure 2.1. Proportion of defensive behaviors employed by incubating northern bobwhites (*Colinus virginianus*) on 3 plantations in southern Georgia and northern Florida, 1999-2006. Types of defensive behavior are represented by the following: direct attack (Att), direct attack/broken wing (Att/Bw), broken wing (Bw), brokenwing/posture/pacing (Bw/Pos/Pac), pecking/attack/pacing (Peck/Att/Pac), posture/pacing (Pos/Pac).

## Depredation and Defense Characteristics by Predator Species

Nest-predator demographics varied across incubation. As incubation progressed, depredations by mammals decreased. Snakes depredated the highest percentage of nests in middle incubation (days 9-16), and fire ants were most active in late incubation (days 17-24) (Figure 2.2).

*Snakes*-Snakes (n=92) accounted for more depredations than any single species. Bobwhites defended the clutch against snakes during 36% (25 of 69) of depredations. Bobwhites directly attacked snakes 44% (11 of 25) of the time. Broken wing behaviors, either alone or combined with direct attack, accounted for 68% (17 of 25) of engagements. One defensive event involving direct attack/broken wing was successful and resulted in the snake fleeing the area without entering the nest bowl. In 28% (7 of 25) of events, the bobwhite engaged the snake by pecking, pacing, or posturing. In at least 13 events, the bobwhite was not present at the nest when the depredation began. In most of these, the bobwhite was away from the nest on recess. We observed one instance of a bobwhite engaging in posturing behavior against a depredating king snake. The snake caught the bird and began constricting. The bobwhite eventually escaped and remained near the nest (in camera view) for the duration of the depredation event.

Snake depredations declined as the nesting season progressed, with 43% (40 of 92) occurring early in the nesting season. The middle and late nesting periods accounted for 32% (29 of 92) and 24% (22 of 92) of snake depredations, respectively. With regards to period of incubation, 36% (33 of 92) of snake depredations occurred early in incubation, followed by 41% (38 of 92) in middle incubation, and 23% (21 of 92) late. Snakes averaged 29.8 (SE=2.8) minutes to depredate a nest.

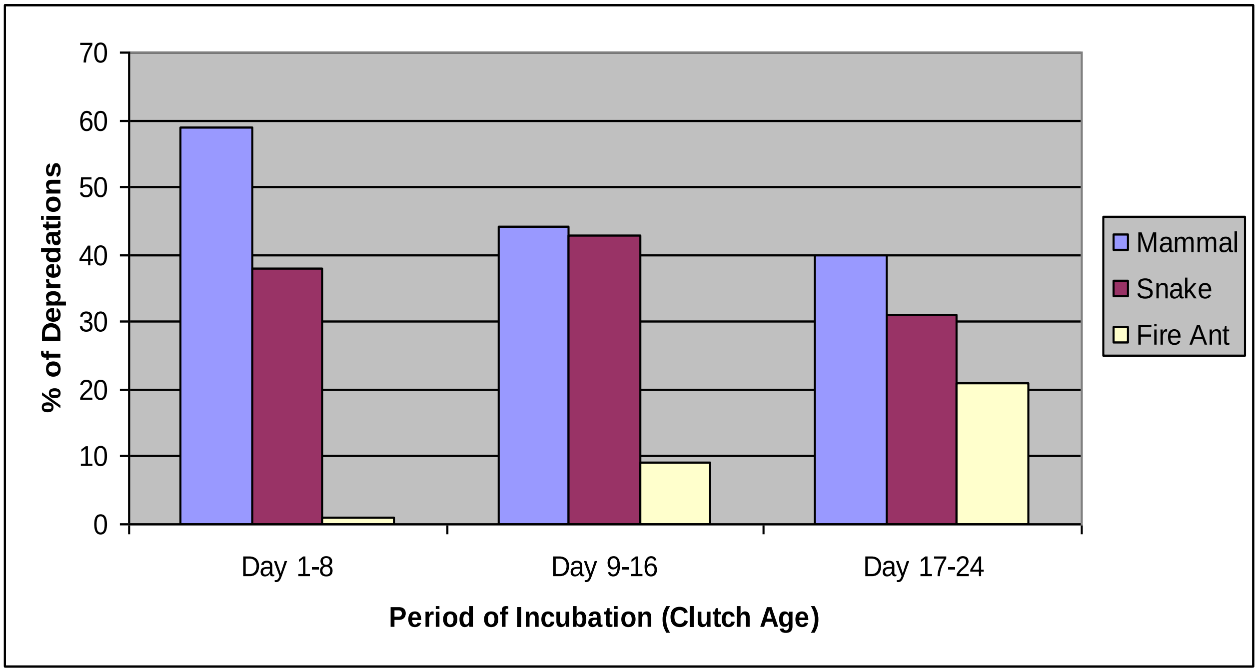

Figure 2.2. Proportion of depredations by predator group occurring at each period of incubation among incubating northern bobwhites (*Colinus virginianus*) (sexes combined) on 3 plantations in southern Georgia and northern Florida, 1999-2006.

*Armadillos*- Bobwhites defended against armadillos (n=33) 70% (16 of 23) of the time. Of these defenses, direct attack accounted for 44% (7 of 16) of defensive events. Broken wing behaviors, either alone or in conjunction with a direct attack, accounted for 88% (14 of 16) of defensive responses. On 5 occasions, the bobwhite circled or paced around the armadillo, often staying within camera view while the depredation occurred. We observed one successful defense against an armadillo. The bobwhite came off the nest and engaged the armadillo with attack/broken wing behaviors before the armadillo reached the nest bowl. This seemed to startle the armadillo and succeeded in deterring the predator.

Armadillos averaged 12.1 (SE=1.26) minutes to depredate nests. Of the 33 armadillo depredations we observed, 45% (15 of 33) occurred late in the nesting season. Early season and middle season had 36% (12 of 33) and 18% (6 of 33) of depredations, respectively. Armadillo depredations declined slightly as incubation progressed with 73% (24 of 33) of depredations occurring in early and middle incubation. Only 27% (9 of 33) of events occurred late in incubation. Armadillos are primarily nocturnal, and all but three armadillo depredations occurred between 21:00 and 07:00 hours. As a result, the incubating bobwhite was present at all depredations with the exception of two that occurred during the daytime.

*Fire Ants*- Bobwhites defended the nest against 83% (10 of 12) of ant depredations. In every ant defense, the bobwhite responded by vigorously pecking at the ants. Frequently (8 of 10 times) the bobwhite also paced in and out of the nest while pecking ants. On 7 of 12 occasions, the bird was away from the nest foraging when the depredation began. We observed one successful ant defense in which the parent returned from recess and pecked the ants out of the nest bowl for 23 minutes before resuming incubation. This occurred in the middle stage of incubation and the nest was ultimately successful.

Of the 22 fire ant depredations viewed, 95% (21 of 22) occurred in middle and late incubation. Of these 22 events, 59% (13 of 22) occurred in the late period of incubation. The middle part of the nesting season had the most ant depredations at 45% (10 of 22), followed by the late season with 27% (6 of 22) and early season with 27% (6 of 22). Fire ant depredations averaged 81.1 (SE=31.4) minutes in length from the time the bird responded to the ants until the time it resumed incubation or abandoned the nest. This depredation length is likely underestimated, due to the difficulty of observing ants and bobwhites in the nest bowl and thus determining start time. However, our observation of 118 other nests (Chapter III) did not identify any missed depredations beyond those previously described from field and camera data.

*Squirrels*-We observed four squirrels at bobwhite nests. Squirrel events averaged 4 (SE=3) minutes in length. Of the four events, two occurred in early season, and two in the middle nesting season. The bobwhite was present at each event and responded with direct attack to 50% (2 of 4) squirrel encounters. The two attacks resulted in successful defenses, as the squirrel was chased from the area without successfully consuming eggs. The two events in which there was no defense by the bobwhite resulted in nest failure; one by the fox squirrel, and one later by an opossum.

*Cotton Rats*-We observed cotton rats near bobwhite nests on numerous occasions. However, on only two occasions did we see any defensive action by the bobwhite toward the rat. Both of these events occurred early in the season, and resulted in a successful defense of the nest. On both occasions, the cotton rat was inside the nest bowl or within centimeters of the nest before the bobwhite defended. In both cases, the bobwhite responded to the cotton rat by direct attack and the events averaged 2.5 (SE=1.5) minutes in duration.

### Parental Characteristics of Defended Nests

To report the frequency of defense by sex of the incubating parent, we assessed only the predator species in which we saw at least one instance of nest defense (e.g. ants, armadillos, snakes, cotton rats, squirrels). Had we factored predation by all species, extraneous variation in the number of non-defended meso-mammalian depredations would likely skew the defense frequencies. Against these defended species, female bobwhites defended 49% (40 of 81) of depredations, and males defended 54.5% (12 of 22) of depredations. However, against the most commonly defended predators (ants, armadillos, and snakes), females defended 88% (7 of 8), 66% (11 of 16), and 39% (22 of 57) of depredations, respectively. Male defense against the same predator suite was 67% (2 of 3), 60% (3 of 5), and 38% (3 of 8), respectively (Figure 2.3).

We observed little difference in the frequency of nest defense between juvenile and adult bobwhites. Against defended predator species, adult and juvenile bobwhites defended 51% (20 of 39, 32 of 63) of depredations, respectively.

### Temporal Defense Characteristics

Relative to the total number of depredations, the proportion of nests defended generally increased as incubation progressed. We observed 17 defenses (31%) during early incubation, 22 defenses (40%) during middle incubation, and 16 defenses (29%) occurred during late incubation (Figure 2.4). We found an increase in defense as the middle stage of incubation approached, and defenses remained proportionally higher than depredations throughout the remainder of incubation.

Conversely, relative to the total number of depredations, nest defense decreased in a linear fashion as the nesting season progressed. The early nesting season produced 28 defenses

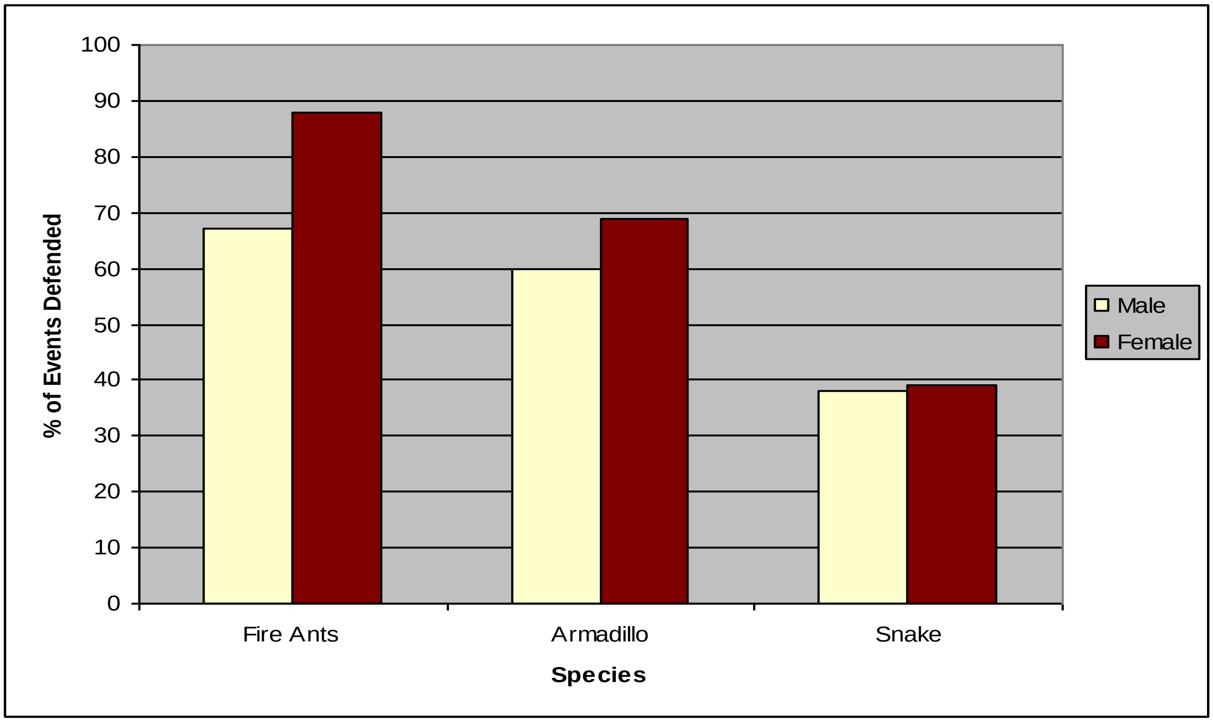

Figure 2.3. Proportion of fire ant (*Solenopsis spp.*), armadillo (*Dasypus novemcinctus*), and snake (*Elaphe spp.* and *Lampropeltis getula getula*) nest-depredation events defended by male or female incubating northern bobwhites (*Colinus virginianus*) on 3 plantations in southern Georgia and northern Florida, 1999-2006.

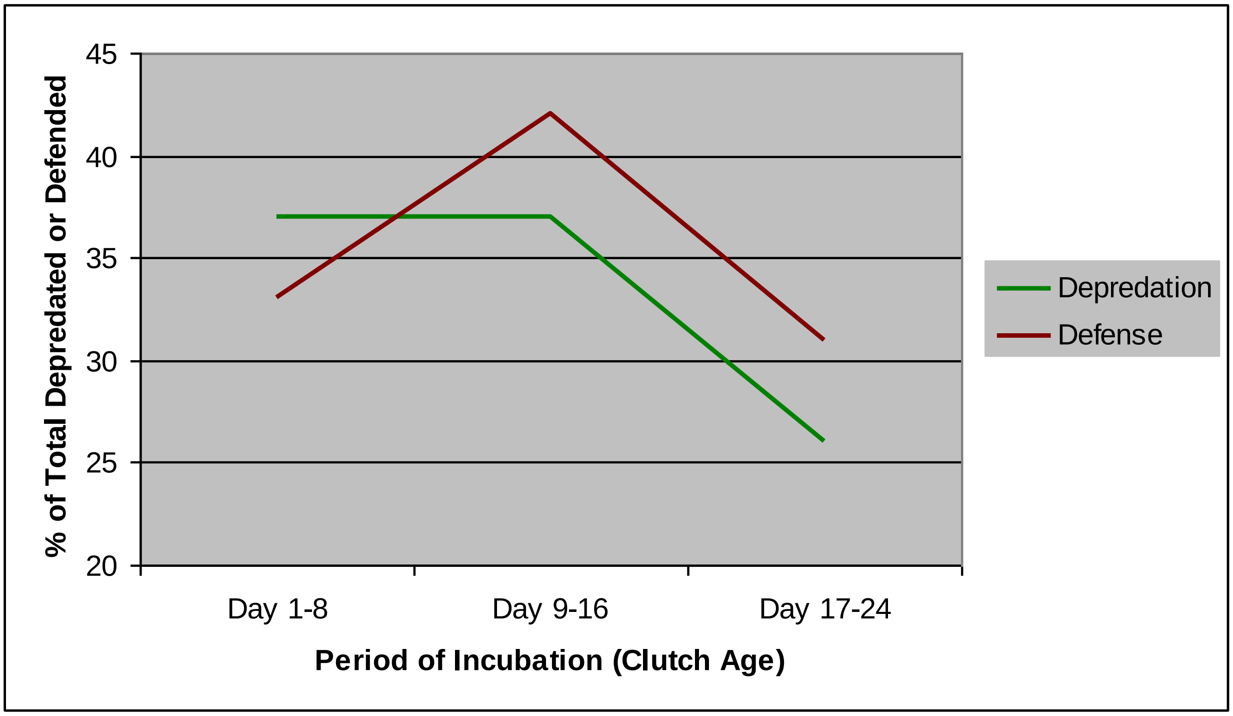

Figure 2.4. Comparison of depredated versus defended nests by period of incubation among incubating northern bobwhites (*Colinus virginianus*) (sexes combined) on 3 plantations in southern Georgia and northern Florida, 1999-2006.

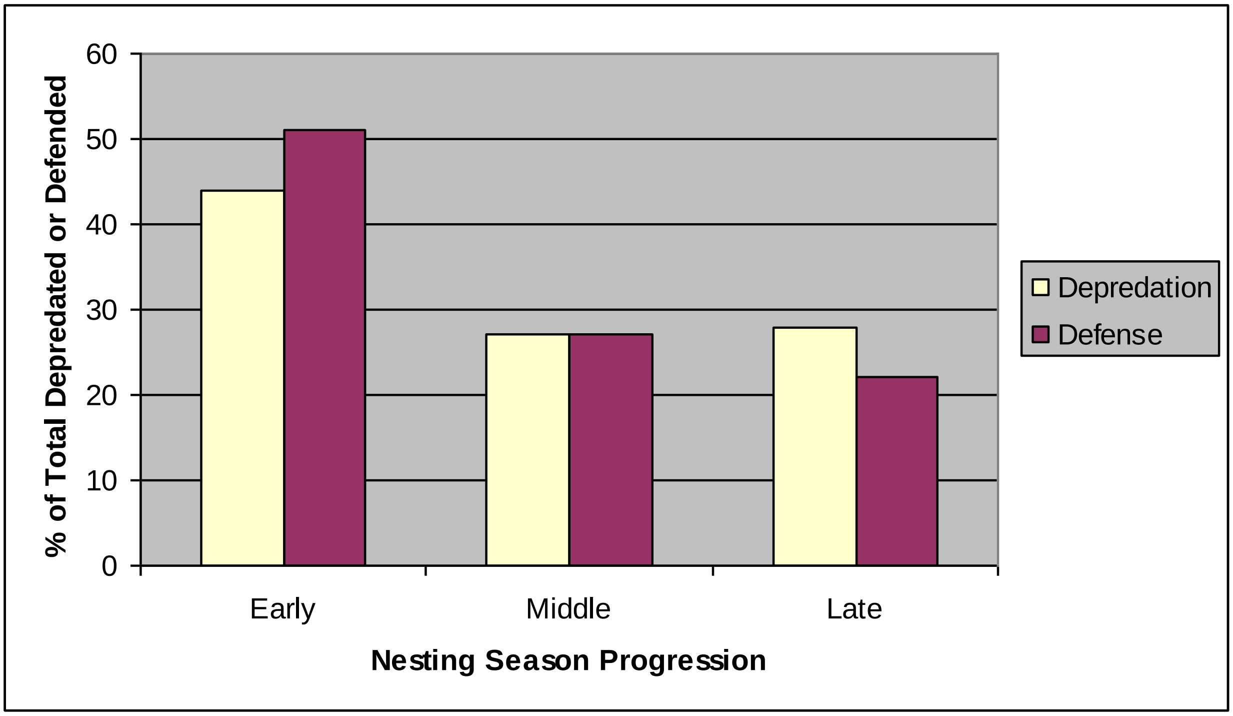

Figure 2.5. Comparison of depredated versus defended nests by early, middle, and late nesting season among incubating northern bobwhites (*Colinus virginianus*) (sexes combined) on 3 plantations in southern Georgia and northern Florida, 1999-2006.

(51%). During the middle and late part of the nesting season, bobwhites defended against 15 depredations (27%), and 12 depredations (22%), respectively (Figure 2.5).

### Flush Distance

If the bobwhite flushed during the depredation event, we estimated the distance from the predator to the nest at flushing when possible. Predictably, predator species influenced flushing behavior among nesting bobwhites. Against armadillos, snakes, and opossums, bobwhites flushed at <0.3 m on 8 (89%), 13 (68%), and 9 (69%) occasions, respectively. Raccoons were >0.3 m from the nest at 23 (96%) flushing events, and 13 (87%) bobcats were >0.3 m from the nest at flushing (Figure 2.6). On 6 occasions, the incubating bird was killed by the bobcat while on the nest or in the process of flushing.

### AIC Model Selection for Likelihood of Defense

Our 95% confidence set included 10 of 31 candidate models. All candidate models (10 out of 10) included in the confidence set contained the parameter PRED in conjunction with various combinations of the other parameters (Table 2.2). The best-fitting model contained PRED + AGE + DOI (Akaike weight = 0.24063; Table 2.2). The next most likely model contained PRED + AGE and received 19.8% of the overall model weight, which comprised 19.80 / 24.06 = 82.3% of the weight of the best-fitting model and was 0.19795 / 0.10771 = 1.84 times more likely than the 3rd best-fitting model (Table 2.2)

Parameter estimates for the model predictors required odds ratio estimation, which we scaled and back transformed for interpretation of biological significance (Table 2.3). Bobwhites were 3.6 times more likely to defend against PRED (snakes/ants) than meso-mammals. As incubation progressed (DOI), the bobwhite was 1.42 times more likely to defend the nest than in the previous, earlier incubation period. AGE was mildly important as adults were 1.25 more likely to defend the nest compared to juveniles. However, females (SEX) were 1.3 times less likely to defend than males. Defense declined slightly as the nesting season progressed, with defense 1.18 times less likely as the nesting season advanced.

## DISCUSSION

We found predator type to be the most important factor in determining the likelihood of nest defense among bobwhites. Of the 11 predator species we observed at bobwhite nests, defensive action was taken against 5. These defended predator types (ants, armadillos, snakes, cotton rats, and squirrels) typically pose little threat to the parent bird, but in most cases are capable of negatively affecting hatching success. We observed no cases of nest defense against species known to at least opportunistically consume bobwhites. Consequently, bobwhites appear able to differentiate between predators that threaten the nest and the parent, and those that only pose a risk to the nest. This perceived threat is likely a determining factor in the bobwhite's response to the predation event. Hatch (1997) found that song sparrow (*Melospiza melodia*) response differed according to nest predator, and that predator species determined whether the birds continued incubation or initiated defensive action. To a degree, this threat recognition is innate but may also be reinforced through experience and interaction with different predators, likely impacting defensive choices (Knight and Temple 1986, Montgomerie and Weatherhead 1988). Regardless, bobwhites are not a "defend at all cost" species. The ability to double-clutch and/or renest enables them to accept the potential loss of a nest but still successfully reproduce at some point in the season. Thus, the decision to defend may be a compromise between self-preservation and the perceived threat to the nest.

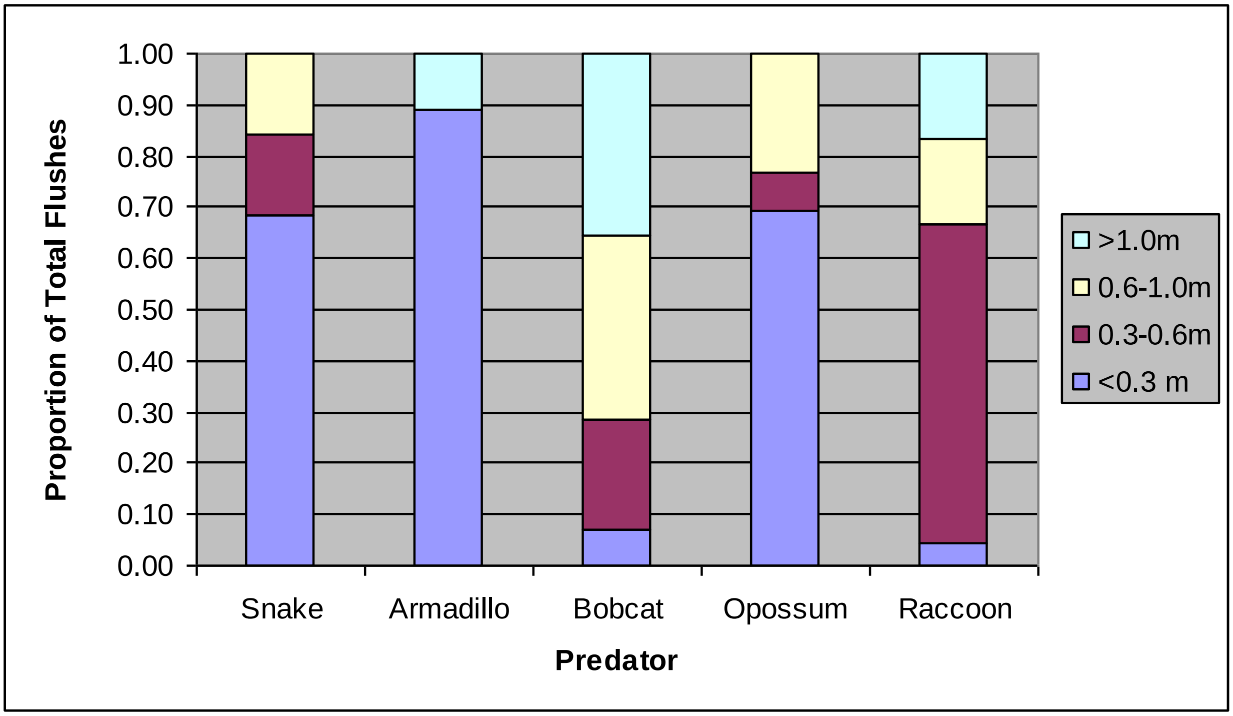

Figure 2.6. Predator distance from northern bobwhite (*Colinus virginianus*) nest (sexes combined) when incubating bobwhite flushed. Data collected on 3 plantations in southern Georgia and northern Florida, 1999-2006. The flushing threshold varied among different predator classes.

Table 2.2. Predictors, number of parameters (K), Akaike's Information Criterion with small-sample size adjustment ($AIC_c$), $\Delta AIC_c$, Akaike weights ($w_i$), and 95% Confidence set for the candidate model set (*i*) used to predict the probability of nest defense among northern bobwhites (*Colinus virginianus*) on 3 plantations in southern Georgia and northern Florida, 1999-2006.

| **MODEL** | **K** | **$AIC_c$** | **$\Delta AIC_c$** | **$w_i$** | **% of max $w_i$** |
|---|---|---|---|---|---|
| PRED+AGE+DOI | 4 | 175.755 | 0.0000 | 0.24063 | 1 |
| PRED+AGE | 3 | 176.145 | 0.3905 | 0.19795 | 0.82 |
| PRED+AGE+DOI+SEASON | 5 | 177.362 | 1.6076 | 0.10771 | 0.45 |
| PRED+AGE+SEASON | 4 | 177.8 | 2.0451 | 0.08655 | 0.36 |
| PRED+SEX+AGE+DOI | 5 | 177.82 | 2.0649 | 0.0857 | 0.36 |
| PRED+SEX+AGE | 4 | 178.027 | 2.2723 | 0.07725 | 0.32 |
| PRED+SEX+DOI | 4 | 179.182 | 3.4269 | 0.04337 | 0.18 |
| PRED+SEX | 3 | 179.314 | 3.5589 | 0.0406 | 0.17 |
| PRED+SEX+AGE+DOI+SEASON(*Global*) | 3 | 179.39 | 3.6354 | 0.03908 | 0.16 |
| PRED+SEX+AGE+SEASON | 5 | 179.623 | 3.8686 | 0.03478 | 0.14 |

Table 2.3. Model-averaged parameter estimates, standard error, odds ratio, and 90% confidence interval used to predict the probability of nest defense among northern bobwhites (*Colinus virginianus*) on 3 plantations in southern Georgia and northern Florida, 1999-2006.

| | | | | **90% CI for Odds Ratio** | |
|---|---|---|---|---|---|
| **Parameter** | **Estimate** | **SE** | **Odds Ratio** | **Low** | **Upper** |
| INTERCEPT | -1.64782 | 0.668 | | | |
| PRED | 1.27679 | 0.38706 | 3.5851 | 1.9000 | 6.7636 |
| SEX | -0.26963 | 0.53171 | 0.7637 | 0.3193 | 1.8264 |
| AGE | 0.22109 | 0.39473 | 1.2474 | 0.6529 | 2.3832 |
| DOI | 0.35731 | 0.25019 | 1.4298 | 0.9484 | 2.1546 |
| SEASON | -0.16789 | 0.22778 | 0.8454 | 0.5819 | 1.2283 |

### Defense Characteristics by Predator Species

Only a small percentage of our total depredations were attributed to fire ants. However, we found the highest rates of defense against fire ants (83%), with most ant depredations occurring toward the end of incubation as the chicks were pipping or beginning to hatch. Coincidentally, this is also when investment in the clutch is at a peak, and the energetic cost of nest loss would be at its highest. The presence of the parent at the nest seems to serve in deterring nest loss to fire ants. In events where documented egg loss occurred, most depredations began when the parent bird was away from the nest on foraging recess. This suggests that when a bird is present on the nest, it is able to stem the tide of approaching ants by pecking and removing them as they arrive at the nest. When away from the nest for an extended period of time (as in recess), the ants may become present in numbers that overwhelm the nest and prevent the parent from effectively removing them. Therefore, it may be likely that birds with a higher rate of nest constancy are at less risk for egg loss from fire ants.

Among vertebrates, bobwhites defended most against armadillos and snakes. Of the two predators, armadillos pose less risk to the parent, but arguably the highest risk to the nest and thus have the highest rate of defense. Most armadillo depredations we observed resulted in the loss of all eggs in the clutch, which is supported by the work of Staller et al. (2005) in the same region. Conversely, snakes are known to consume bobwhites and thus pose a greater risk to the parent than armadillos. However, snakes may only consume part of the clutch, resulting in a partial depredation and the chance to successfully hatch at least some eggs. We found snakes were defended against less frequently than armadillos. However, it may be possible that defense rates relative to these 2 species were affected partially by the timing of depredation events. Armadillos were typically nocturnal foragers, which increases the likelihood that the bobwhite will be present on the nest, and thus able to defend. Many snake depredations occurred during the middle of the day when bobwhites were often away from the nest in daily recess. Consequently, in their absence they were unable to defend against these snake depredations. Additionally, Staller et al. (2005) noted that bobwhite defense against snakes was influenced by the size of the snake, with smaller snakes (<1 m in length) being defended against more frequently than larger snakes (>1 m in length). This may influence defense behavior since larger snakes are more likely capable of consuming the attending adult.

Depredation events involving squirrels and cotton rats were much less common (6 events), but normally resulted in the bobwhite defending the nest. Cotton rats in particular were often tolerated around bobwhite nests. We frequently observed cotton rats near nests, both while the parent was present and away on recess. When the parent was away, the rat would often repeatedly enter the nest bowl, but evidently was not able to significantly damage the eggs. One of the 2 cotton rat defenses we noted occurred late in incubation when a bobwhite returned from recess and encountered a rat in the nest bowl. The cotton rat had been near the nest several times prior to the parent leaving and its presence elicited no response. However, upon returning and finding the rat in the nest moving eggs, the bobwhite attacked the rat and drove it away from the nest bowl. This nest later successfully hatched 13 of 14 eggs. From our observations, it appears bobwhites generally do not regard cotton rats as a threat and thus do not frequently defend against them unless the rat is actively attempting to pillage the nest or its contents.

Squirrels have been documented destroying bobwhite nests (Staller et al. 2005), although infrequently. In contrast to cotton rats, which generally pose little threat to bobwhite eggs, squirrels were not typically permitted near the nest. One bird twice engaged a squirrel that was attempting to enter the nest bowl. In the second event, the bobwhite chased the squirrel out of camera view and did not return for over a minute.

Successful nest defense events among bobwhites were infrequent, but did occur. Without video documentation, identifying such events would be nearly impossible; a hatched nest by default leaves little sign of a successful defense. Furthermore, any defensive attempt at a failed nest would necessarily be unsuccessful. Among successful defenses, all but one was aggressively initiated by the bobwhite before the predator gained access to the nest bowl. The bobwhite left the nest and engaged the predator rapidly and aggressively. No successful defense involved passive displays such as posturing or pacing. Most frequently, the predator appeared startled and left immediately without a struggle. In such cases, since the predator was engaged before entering the nest, they may not have been aware of the nest and thus never returned. Conversely, defensive attempts that were initiated once the predator gained access to the eggs were almost always unsuccessful.

### Parental Characteristics of Defended Nests

Overall, male bobwhites defended at a slightly higher rate than females. Stoddard (1931) also noted the particular aggressiveness with which males defended nests. Brunton (1990) described a more intense defensive response by male killdeer (*Charadrius odiferous*), a bird with precocial young like the bobwhite. However, studies on other bird species have shown both no difference in defense rates between the sexes or higher rates of female defense (Sergio and Bogliani 2001, Tryjanowski and Golawski 2004). As uniparental incubators, incubation is certainly expensive for the male bobwhite. Incubation and nest attendance necessarily limit additional mating opportunities, and attending males may be more subject to predation than their non-incubating counterparts. However, the male may be in better physical condition than the female when incubation begins if she has been weakened by egg production and laying. This decrease in female energy reserves may be an underlying factor influencing defense rates between the sexes (Montgomerie and Weatherhead 1988).

Aside from investment theory, hormonal influences affect sex-specific nest defense behaviors. Testosterone levels have been shown to influence reproductive effort in male birds by decreasing attendance and care of dependent offspring. In a manipulative study conducted on dark-eyed juncos (*Junco hyemalis*), testosterone-treated males were slower to respond to predators and spent less time at the nest than females and control males (Cawthorn et al. 1998). To our knowledge, no research has addressed the level of testosterone in incubating male bobwhites nor the influence of hormone levels on bobwhite nest behavior.

Our smaller male sample size may have also impacted our results. We noted high rates of response against cotton rats and squirrels (4 defenses of 6 encounters), 2 species that only interacted with male birds. Though likely by chance, these encounters increased the proportion of male defensive response. Among more commonly defended species, females defended at a slightly higher rate.

Adult bobwhites were slightly more inclined to defend than were juveniles. Bobwhites are a short-lived species in which survivorship is likely age-independent after the first year. Among such non-senescent species, the intensity or frequency of nest defense should not vary strictly with age, but also as a result of greater nesting experience (Montgomerie and Weatherhead 1988). As a parent gains experience, the cost for a given level of defense decreases. Since adult bobwhites have probably survived several nesting opportunities, they are likely more experienced than a juvenile bird entering its first nesting season. This experience may translate to better recognition of the threat posed by a nest predator and result in more frequent and efficient nest defense.

**Temporal Characteristics of Defended Nests**

We found bobwhites more likely to defend the nest as incubation progressed. An increase in investment throughout incubation has previously been noted in bobwhites, especially with regards to the reluctance to abandon a nest in late incubation (Rosene 1969). Likewise, an increase in defense as incubation progresses has been shown in other, primarily altricial species (East 1981, Shields 1984, Merritt 1984). Early in incubation, the parent has less invested in the nest and as a result, energetic costs and the corresponding value of the clutch are relatively low. As incubation progresses, the clutch becomes increasingly valuable and the probability of defense increases. In birds with precocial young, such as bobwhites, nest defense should peak near hatching because that is when the chicks leave the nest (Montgomerie and Weatherhead 1988).

With regards to bobwhite defense throughout incubation, we also noted several temporal patterns and tendencies among predators that may influence defense frequency. For example, we reported the lack of nest defense against raccoons, opossums, and bobcats. These meso-mammals are quite efficient in food acquisition and tend to find local bobwhite nests relatively early in incubation. Conversely, snakes and fire ants are somewhat less mobile and may not range as far in pursuit of food. Though present in higher densities than mammal predators, the common snake predators of bobwhites in this region tend to spend a great deal of time sitting and may only be actively foraging for a couple days of the >3 week incubation period of a nest. As a result, they tend to take longer to find nests and often depredate nests later in incubation. Hence, if species that are frequently defended against are primarily depredating nests in late incubation, and non-defended species predominate in early incubation, then there will be an increase in defense as incubation progresses. Although this doesn't solely account for our results, the predator context of an area may certainly influence the timing of depredation patterns, nest defense frequency, and cost to the incubating parent.

Bobwhites are persistent renesters and may nest several times each season (Stanford 1972). As the nesting season progressed, we noted a slight decrease in nest defense which our predictor models supported. This is in conflict with the renesting potential hypothesis which states that defense should increase throughout the nesting season until the opportunity to renest is eliminated (Barash 1975). Instead, we see a linear decrease in defense as autumn approaches, regardless of reported nest attempt. Bobwhites may begin nesting as early as April, and nest building, egg-laying, and incubation are energetically expensive endeavors. A bobwhite nesting in September may have attempted several nests throughout the season and could possibly have 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(s) were destroyed well into incubation, then the bird's physical condition may have declined all the more.

### Flush Distance

The distance of a predator from the nest before the bobwhite flushed varied greatly among predator species. This threshold distance varies somewhat according to the mobility and armament of the predator (Montgomery and Weatherhead 1988). The more mobile the predator, the earlier the bobwhite would need to flush or defend. Thus, the threshold distance for a snake or ant should be less than that for a mammalian predator such as a bobcat. Accordingly, the predators most dangerous to the bobwhite itself generally had the greatest threshold distance. Bobwhites tolerated bobcats and raccoons the least. Snakes, armadillos, and opossums were allowed to approach closer before flushing, if the bird flushed at all. Opossums have been known to kill an adult bobwhite (Staller et al. 2005), so the proximity with which they are allowed to approach the nest is surprising. We theorize it is related to their pattern of locomotion while foraging. Compared to bobcats and raccoons, which are more deliberate, opossums tend to wander when seeking food. Much like an armadillo, they are likely not perceived as a threat until they reach the nest bowl.

Often, the act of the bobwhite flushing seemed to startle the predator, particularly mammalian predators. The predator would briefly pursue the bird before returning to search for the nest. On 3 separate occasions we observed an armadillo, bobcat, and raccoon within a meter of a bobwhite nest. However, the bird was away on recess and the predator never discovered the nest. Had the bird been present and flushed, the nest would likely have been discovered and destroyed.

## Conclusions

As suggested by investment theory and related research, bobwhite nest defense clearly varies according to parental characteristics, predator species, and various temporal factors. Many of the correlates affecting nest defense and parental investment in this study would vary across different regions of the country, but the results should be representative of bobwhites as a species.

A great deal of research has been conducted on avian nest defense and parental investment, but there is a relative paucity of such work on ground-nesting birds, particularly in the order Galliformes. An area that deserves further research is the importance of hormones, particularly testosterone and prolactin, on nesting behavior in bobwhites and other Galliformes. It would be difficult to conduct this research on wild bobwhites, but similar research on waterfowl and passerine species could provide a framework for a manipulative experimental design. Although research into behavioral ecology does not necessarily address management concerns, it is nevertheless valuable in identifying the underlying mechanisms responsible for a species life history requirements, behavior, and ecology.

## LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* Proceedings of Second International Symposium on Information Theory. B.N Petrov and F. Csaki, editors. Akademiai Kiado, Budapest, Hungary.

American Ornithologists' Union. 1988. Report of committee on use of wild birds in research. Auk 105 (1, Supplemental): 1-41.

Barash, D.P. 1975. Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. Wilson Bulletin 87:367-373.

Biermann, G.C., and R.J. Robertson. 1981. An increase in parental investment during the breeding season. Animal Behaviour 29:487-489.

Brennan, L.A. 1999. Northern bobwhite *Colinus virginianus.* In the Birds of North America No. 397. A. Poole and F. Gill, editors. The Birds of North America, Inc., Philadelphia, PA, USA.

Brown, K.P., H. Moller, J. Innes, and P. Jansen. 1998. Identifying predators at nests of small birds in a New Zealand forest. Ibis 140:272-279.

Brunton, D.H. 1986. Fatal antipredator behavior of a killdeer. Wilson Bulletin 98:605-607.

Brunton, D.H. 1990. The effects of nesting stage, sex, and type of predator on parental defense by killdeer (*Charadrius vociferous*): testing models of avian parental defense. Behavioral Ecology and Sociobiology 26:181-190.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and inference: an information-theoretic approach. Springer-Verlag, New York, NY.

Cawthorn, J.M. and D.L. Morris, E.D. Ketterson, and V. Nolan, Jr. 1998. Influence of experimentally elevated testosterone on nest defence in dark-eyed juncos. Animal Behaviour 56: 617-621.

Church, K.E., J.R. Sauer, and S. Droege. 1993. Population trends of quails in North America. Proceedings of the National Quail Symposium 3:44-54.

East, M. 1981. Alarm calling and parental investment in the robin *Erithacus rubecula*. Ibis 123:223-230.

Ghalambor, C.K. and T.E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Animal Behaviour 60:263-267.

Gochfeld, M. 1984. Antipredator behavior: aggressive and distraction displays of shorebirds. Pp. 289-377 *in* J. Burger and B.L. Olla, Editors. Shorebird Breeding Biology and Populations. Plenum Press, New York.

Guthery, F.S. 1997. A philosophy of habitat management for northern bobwhites. Journal of Wildlife Management 61:291-301.

Hatch, M.I. 1997. Variation in song sparrow nest defense: Individual consistency and relationship to nest success. Condor 99:282-289.

Hosmer, D.W., Jr. and Lemeshow, S. 1989. Applied logistic regression. John Wiley & Sons, New York.

Knight, R.L., and S.A. Temple. 1986. Why does the intensity of avian defense increase during the nesting cycle? Auk 103:318-327.

________________________. 1988. Nest-defense behavior in the red-winged blackbird. Condor 90:193-200.

Lind, J. and W. Cresswell. 2005. Determining the fitness consequences of antipredation behavior. Behavioral Ecology 16:945-956.

Mallory, M.L., D.K. McNicol, and R.A. Walton. 1998. Risk-taking by incubating common goldeneyes and hooded mergansers. Condor 100:694-701.

Merritt, P.G. 1984. Observer recognition by the northern mockingbird. Journal of Field Ornithology 55:252-253.

Montgomerie, R.D. and P.J. Weatherhead. 1988. Risks and rewards of nest defence by parent birds. The Quarterly Review of Biology 63:167-187.

Newton, I. 1998. Population limitation in birds. Academic Press Limited, San Diego, CA, USA.

Pettingill, O.S., Jr. 1976. Observed acts of predation on birds in northern lower Michigan. Living Bird 15:33-41.

Pugesek, B.H. 1983. The relationship between parental age and reproductive effort in the California gull (*Larus californicus*). Behavioral Ecology and Sociobiology 13:161-171.

Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.

___________. 1973. Ecology. Chiron Press, New York.

Rollins, D., and J.P. Carroll. 2001. Impacts of predation on northern bobwhite and scaled quail. Wildlife Society Bulletin 29:39-51.

Rosene, W. 1969. The bobwhite quail: its life and management. Rutgers University Press, New Brunswick, New Jersey.

Sandercock, B.K. 1994. The effect of manipulated brood size on parental defence in a precocial bird, the willow ptarmigan. Journal of Avian Biology 25:281-286.

Sergio, F. and G. Bogliani. 2001. Nest defense as parental care in the northern hobby (*Falco subbuteo*). Auk 118:1047-1052.

Shields, W.M. 1984. Barn swallow mobbing: self-defence, collateral kin defence, group defence, or parental care? Animal Behavior 32:132-148.

Smith, H.D., F.A. Stormer and R.D. Godfrey, Jr. 1981. A collapsible quail trap. Rocky Mountain Forest and Range Experiment Station. Research Note RM-400. 3 pp.

Staller, E.L., W.E. Palmer, J.P. Carroll, R.P. Thornton, and D.C. Sisson. 2005. Identifying predators at northern bobwhite nests. Journal of Wildlife Management 69:124-132.

Stanford, J.A. 1972. Second broods in bobwhite quail. Proceedings of the National Bobwhite Quail Symposium 1:199-204.

Stoddard, H.L. 1931. The bobwhite quail: its life history and management. Charles Scribner's Sons, New York, USA.

Thornton, R. 2003. The experimental effect of mesomammal predator removal on nest depredation of northern bobwhite in south Georgia and north Florida. M.S. Thesis, University of Georgia, Athens.

Tryjanowski, P. and A. Golawski. 2004. Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season. Journal of Ethology 22:13-16.

White, C.G. and R.A. Garrott. 1990. Analysis of radio-tracking data. Academic Press, San Diego, CA. 383 pp.

Whittam, R.M., and M.L. Leonard. 2000. Characteristics of predators and offspring influence nest defense by arctic and common terns. Condor 102:301-306.

Williams, C.K., F.S. Guthery, R.D. Applegate, and M.J. Peterson. 2004. The northern bobwhite decline: scaling our management for the twenty-first century. Wildlife Society Bulletin 32:861-869.

# CHAPTER 3

# USING CONTINUOUS VIDEO TO MONITOR PATTERNS OF INCUBATION BEHAVIOR IN NORTHERN BOBWHITES (*COLINUS VIRGINIANUS)*[1]

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[1] Burnam, J.S, G. Turner, S.N. Ellis-Felege, W.E. Palmer, D.C. Sisson, and J.P. Carroll. To be submitted to Journal of Avian Biology.

## INTRODUCTION

Very little is known about the daily attendance rhythms and behavioral patterns of incubating northern bobwhites (*Colinus virginianus*; hereafter, bobwhite). 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 North America (Guthery 1997, Williams et al. 2004). However, relatively little research has been conducted on the behavioral ecology of nesting bobwhites, particularly relevant to daily patterns of nest recess, attendance, and parental investment.

Parental investment is an underlying mechanism that influences incubation decisions and 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 investment behaviors, including reproductive ecology, sex and age of parent, habitat quality, clutch age, and whether it is early or late in the nesting season (Trivers 1972, Moller 1991, Rauter and Reyer 1997).

The energetic costs of incubation are high (Monaghan and Nager 1997), and birds are likely constrained from attending more due to the depletion of energy reserves (Cresswell et al. 2004). Since 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 trade-off between meeting the metabolic needs of the parent, minimizing predation risk, and maintaining a suitable environment for the developing embryos (Afton 1980, Flint and Grand 1999). A parent bird's ability to balance daily energetic needs with embryo requirements is a continual struggle influenced by the 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).

Though 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. Gloutney et al. (2004) found that recess times among Ross's and lesser snow geese (*Chen rossii* and *Chen caerulescens,* respectively) varied widely by reproductive stage and food intake. Likewise, incubation initiation has been shown to vary among conspecifics with regards to individual body condition and egg size (Hanssen et al. 2002).

The northern bobwhite is a cryptic, ground-nesting bird in the order Galliformes. 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. Stoddard (1931) 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.

We wanted to directly observe bobwhite incubation behavior to quantify patterns of nest recess and attendance along a spectrum that includes sex and age of the incubating parent as well as a variety of daily and seasonal correlates. We predicted varying daily recess length associated with parent sex, nesting season progression, and clutch age.

## METHODS

### Study Site

Our study area consisted of 3 sites. Tall Timbers Research Station is located in northern Florida and Pebble Hill Plantation and Pinebloom Plantation are in southwestern Georgia. 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 (*Pinus palustris*) and shortleaf pine (*Pinus 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 (Thornton 2003). Fall covey counts estimate 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.

From 1999 to 2006, bobwhites were captured from January to April using baited "walk in" funnel traps (Smith et al. 1981). Captured bobwhites were classified by age and sex, and fitted with 6.5g pendant-style radio-transmitters (Staller et al. 2005). All procedures involved in trapping, handling, and banding captured birds followed the guidelines presented in the American Ornithologists' Union Report of Committee 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). Bobwhites were monitored on a daily basis and assumed to be nesting when in the same location for 2 consecutive days. Nests were then located using telemetry homing techniques (White and Garrott 1990).

### Camera System

We installed continuous-recording, near-infrared video cameras at bobwhite nests and monitored the birds throughout incubation. The video camera system was comprised of a N9C2 Fieldcam LRTV Microcam with a 3.7mm wide-angle lens and a 6-array LED at 950 nm (Furman Diversified, Inc.). Sunlight provided ample 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. A

VHS time-lapse recorder that continuously recorded 20 frames per second was connected to the camera and illumination system. Since the recording rate was 1/3 normal speed, each 8 hour tape lasted 24 hours (Staller et al. 2005).

The cameras were installed 1.5 – 2 m from the nest bowl while the incubating parent was away. Modification of vegetation was minimized and the camera and components were camouflaged for minimum disturbance. Care was taken to prevent cables and cords from crossing likely predator travel routes such as firebreaks and roads (Staller et. al 2005). After installing the camera, the nest was monitored every 1-2 hours to ensure the bird returned to resume incubation. If the bird had not returned within 4-6 hours, the camera was adjusted and placed at an angle to the nest to further minimize disturbance to the incubating bird. A technician replaced tapes and batteries every 24 hours until nesting was complete or the nest was depredated. Tapes were labeled with the individual bird identification number for use in acquiring bird-specific information for data analysis.

### Data Collection

We selected a random sample of 118 birds (male=56, female=62) 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 of the bird (adult/juvenile), site (plantation), date, number of recesses taken (if any), recess start time and duration, period of incubation, 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. Nest absences of less than a minute were not considered recess events as bobwhites occasionally leave the nest during the day for brief periods. We categorized period of incubation as early (day 1-8), middle (day 9-16), and late (day 17-24). 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 indicated the bird was stationary and incubating. 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 the 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. We constructed hierarchical models using the PROC MIXED procedure from SAS software (SAS Institute 2003). PROC MIXED allows for the incorporation of different level predictors into the candidate models and allowed us to avoid the pseudoreplication caused by assuming that repeated observations on the same bird were independent (Hurlbert 1984).

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 3.1). We created 23 candidate model sets from the global prediction model that we perceived as being biologically relevant combinations of predictors. We used Akaike's Information Criterion (Akaike 1973, Burnham and Anderson 2002) in the model selection process to determine the combination of predictors that most influenced daily recess length. We then calculated AIC values with the adjustment for small sample size ($AIC_c$) (Burnham and Anderson, 2002) for each predictor model.

Table 3.1. Explanation of variables used to model daily nest recess length among northern bobwhites (*Colinus virginianus*) on 3 plantations in southern Georgia and northern Florida, 1999-2006.

| **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. |

In addition to the analyses above, we compiled basic descriptive statistics using proportions (%) and means with standard error (SE) to further evaluate our findings.

## RESULTS

We monitored daily nest-video footage for 56 male and 62 female bobwhites (n=118). We directly viewed a total of 847 nest-days representing 20,328 hours 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 7-year study (incubated nests only) was 60% (429 of 714). Mean clutch size among our sample nests was 12.6 (SE=0.3) eggs.

### Temporal Distribution of Recess Events

We observed 36% (302 of 847) of our recess events occurred 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 (Appendix 3A). Across incubation, 24% (201 of 847) of observed recess events occurred in early incubation (Day 1-8). The middle (Day 9-16) and late incubation periods (Day 17-24) accounted for 46% (393 of 847) and 30% (253 of 847) of recesses, respectively (Appendix 3A). The difficulty in locating and promptly monitoring bobwhite nests early in incubation limited our observations for this period. Additionally, the high rate of nest depredations among bobwhites constrained our late incubation observations because many nests did not survive to the hatching stage.

### Daily Recess Frequency and Start Time

A single recess event was most common at 87% (733 of 847) of days (sexes combined). Bobwhites engaged in 2 or more daily recesses on 9% (74 of 847) of days, and 0 recesses were

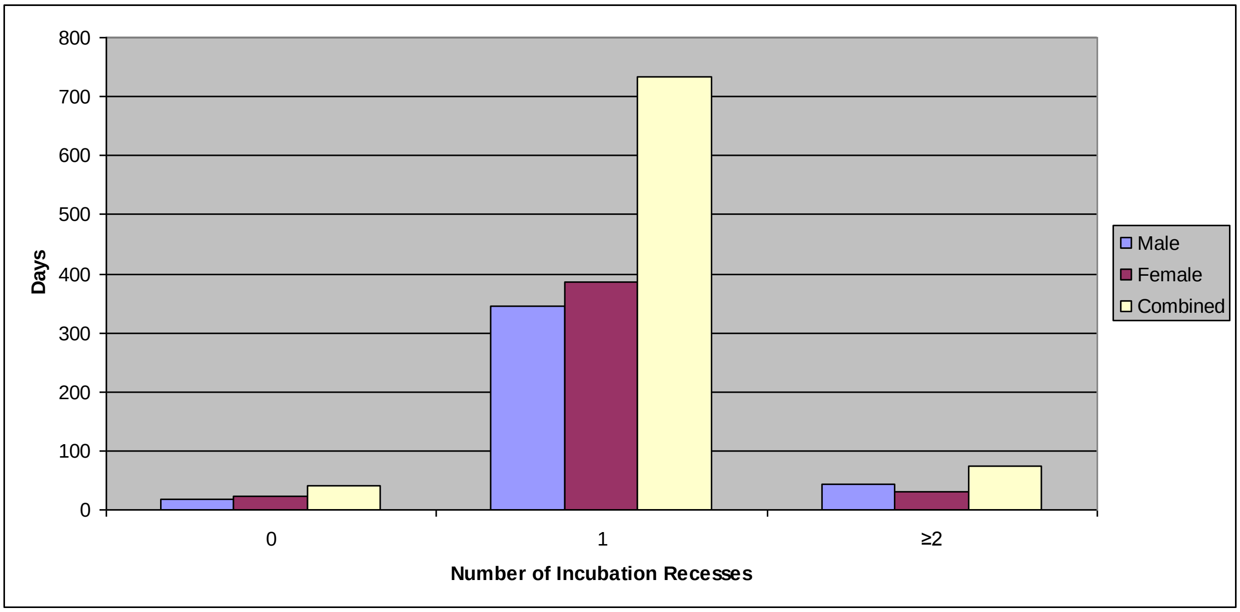

Figure 3.1. Number of 0, 1, and ≥ 2 daily incubation recesses taken by male, female, and combined northern bobwhites (*Colinus virginianus*) for 118 nests on 3 plantations in southern Georgia and northern Florida, 1999 – 2006.

observed on 5% (40 of 847) of days (Figure 3.1, Appendix 3A). We observed >2 daily recesses on only 4 of 847 days. Thus, we combined these observations into a “2 or more” daily recess category for analysis. Because bobwhites are cryptic and nest on the ground in typically dense vegetation, our observations of days in which 0 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, unviewable direction.

Males (median start time=14:00) consistently initiated recess earlier in the day than females (median start time=15:00) (Figure 3.2). Additionally, males (64%) were more likely than females (57%) to leave the nest for recess via flight rather than walking away.

### Recess Duration

Mean total daily recess length was 182 (SE=43) minutes for hatched nests and 224 (SE=43) minutes for failed nests. Among failed nests, bobwhites engaged in 2 or more recesses on 14% (35 of 250) of days compared to 6% (32 of 533) of days for hatched nests. There was no difference in total daily recess length between males (204 minutes, SE=49) and females (186 minutes, SE=49), nor among birds that took 1 recess per day (201 minutes, SE=47) and birds who took 2 or more recesses per day (223 minutes, SE=48). Recess events on rainy days were 188 (SE=56) minutes in duration, and those taken on clear days averaged 207 (SE=49) minutes.

### Mixed Model Analysis and Model Selection for Recess Length

Our 95% confidence set was represented by 2 of 23 candidate models. However, because all covariates were contained within at least 1 of the top 2 models, we believe it relevant to include every different factor combination that mildly affected recess length. Therefore, we included the 9 candidate model sets displaying any calculated Akaike weight to serve in a comparative function for analyzing the importance of each covariate and covariate combination (Table 3.2).

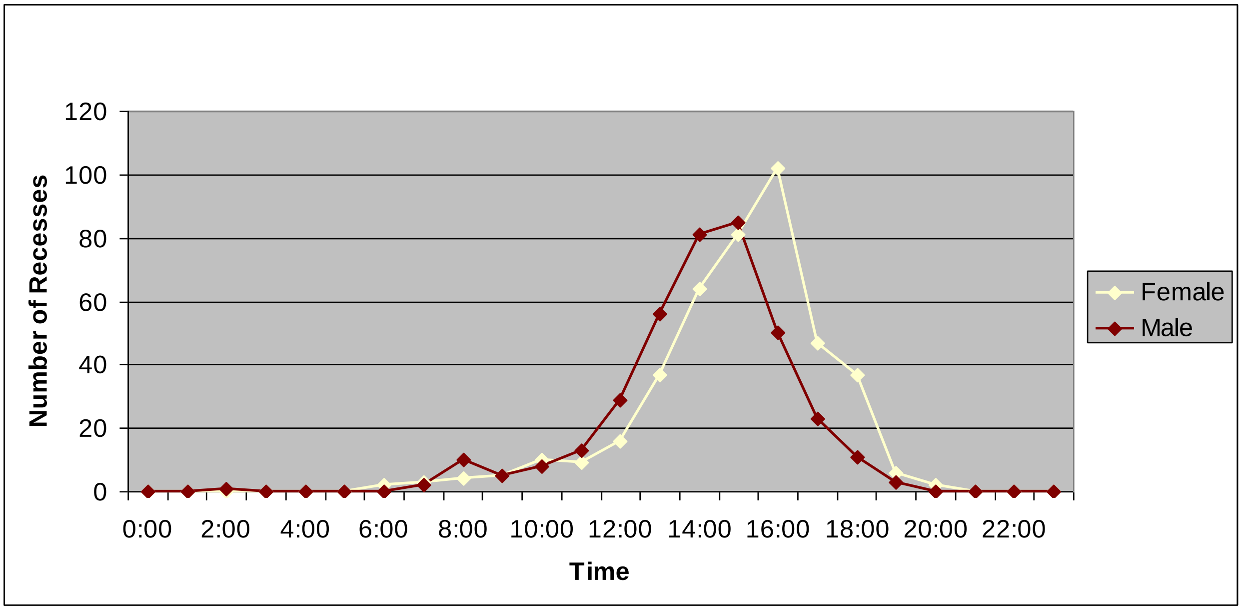

Figure 3.2. Start time of first daily nest recess by male and female northern bobwhites (*Colinus virginianus*) on 3 plantations in southern Georgia and northern Florida, 1999 – 2006. Males (median start time =14:00) consistently initiated recess earlier in the day than females (median start time =15:00).

Table 3.2. Predictors, number of parameters (K), Akaike's Information Criterion with small-sample size adjustment ($AIC_c$), $\Delta AIC_c$, and Akaike weights ($w_i$), for the models containing any weight in the candidate model set ($i$) used to explain daily nest recess length among northern bobwhites (*Colinus virginianus*) on 3 plantations in southern Georgia and northern Florida, 1999-2006.

| **MODEL** | **K** | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| CLUTCH + SEASONMID + SEASONLATE + POIMID + POILATE | 8 | 8643.03 | 0.000 | 0.69179 |
| CLUTCH + SEX + AGE + POIMID + POILATE +SEASONMID +SEASONLATE (*Global)* | 10 | 8644.65 | 1.623 | 0.30722 |
| CLUTCH + SEX + SEASONMID + SEASONLATE | 7 | 8658.58 | 15.547 | 0.00029 |
| CLUTCH + SEASONMID + SEASONLATE | 6 | 8659.22 | 16.197 | 0.00021 |
| CLUTCH + POIMID + POILATE | 6 | 8659.95 | 16.920 | 0.00015 |
| CLUTCH + SEX + AGE + SEASONMID + SEASONLATE | 8 | 8660.45 | 17.419 | 0.00011 |
| CLUTCH + SEX + POIMID + POILATE | 7 | 8660.51 | 17.481 | 0.00011 |
| CLUTCH + AGE + POIMID + POILATE | 7 | 8661.45 | 18.419 | 0.00007 |
| AGE + POIMID + POILATE + SEX + CLUTCH | 8 | 8662.13 | 19.104 | 0.00005 |

The best-fitting model contained CLUTCH + SEASONMID + SEASONLATE + POIMID + POILATE (Akaike weight = 0.69179; Table 3.2). The next most likely model was our global model (CLUTCH + SEX + AGE + POIMID + POILATE + SEASONMID + SEASONLATE; Akaike weight = 0.30722; Table 3.2) which was 0.69179 / 0.30722 = 2.25 times less likely than the best fitting model (Table 3.2).

Parameter estimates for SEASONMID and SEASONLATE suggest that the progression of the nesting season had a positive effect on recess length (Table 3.3, Figure 3.3, and Appendix 3B). Conversely, parameter estimates for POIMID and POILATE suggest a negative effect on recess length as incubation progresses (Table 3.3, Figure 3.3, and Appendix 3B). Essentially, recess length is expected to increase as the nesting season progresses and to decrease as incubation advances and the clutch ages. Clutch size (CLUTCH), sex of parent (SEX), and age of parent (AGE) did not significantly affect recess length in any model (Table 3.3).

## DISCUSSION

We noted 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 daily and seasonal in nature and related primarily to incubation and nesting season stage.

### Recess Frequency and Start Time

Regardless of sex, most bobwhites engaged in 1 recess event per day. Two recesses were occasionally taken, and less frequently 0 recesses were observed. Stoddard (1931) noted

Table 3.3. Estimates, standard error, 95% confidence interval, and p-value (α = 0.05) for parameters included within models containing weight from the candidate model set used to explain daily nest recess length among northern bobwhites (*Colinus virginianus*) on 3 plantations in southern Georgia and northern Florida, 1999 – 2006.

| | | | **95% CI** | | |
|---|---|---|---|---|---|
| **Parameter** | **Estimate** | **SE** | **Lower** | **Upper** | **P-value** |
| CLUTCH + SEASONMID + SEASONLATE + POIMID + POILATE | | | | | |
| Intercept | 164.4900 | 32.3238 | 100.1500 | 228.8300 | <0.0001 |
| CLUTCH | 1.7148 | 2.2988 | -2.8012 | 6.2308 | 0.4560 |
| SEASONMID | 51.7955 | 13.1738 | 25.9150 | 77.6760 | <0.0001 |
| SEASONLATE | 43.7616 | 12.4440 | 19.3149 | 68.2083 | 0.0005 |
| POIMID | -25.0520 | 9.1471 | -43.0220 | -7.0820 | 0.0064 |
| POILATE | -33.0392 | 10.8050 | -54.2661 | -11.8123 | 0.0023 |
| CLUTCH + SEX + AGE + POIMID + POILATE +SEASONMID +SEASONLATE (*Global)* | | | | | |
| Intercept | 177.5200 | 33.3283 | 111.1700 | 243.8700 | <0.0001 |
| CLUTCH | 1.5360 | 2.2823 | -2.9477 | 6.0198 | 0.5012 |
| SEX | -12.9368 | 11.0121 | -34.5707 | 8.6972 | 0.2406 |
| AGE | -8.9867 | 12.2592 | -33.0706 | 15.0972 | 0.4639 |
| POIMID | -24.9507 | 9.1381 | -42.9030 | -6.9984 | 0.0065 |
| POILATE | -32.7489 | 10.8150 | -53.9955 | -11.5022 | 0.0026 |
| SEASONMID | 49.6708 | 13.1691 | 23.7994 | 75.5422 | 0.0002 |
| SEASONLATE | 43.5498 | 12.3725 | 19.2433 | 67.8564 | 0.0005 |

Table 3.3 continued.

| | | | 95% CI | | |
|---|---|---|---|---|---|
| **Parameter** | **Estimate** | **SE** | **Lower** | **Upper** | **P-value** |
| CLUTCH + SEX + SEASONMID + SEASONLATE | | | | | |
| Intercept | 162.4700 | 34.4599 | 93.8755 | 231.0600 | <0.0001 |
| CLUTCH | 1.2675 | 2.3922 | -3.4321 | 5.9671 | 0.5964 |
| SEX | -15.9669 | 11.4627 | -38.4858 | 6.5521 | 0.1642 |
| SEASONMID | 45.9679 | 13.4678 | 19.5099 | 72.4258 | 0.0007 |
| SEASONLATE | 37.6379 | 12.6061 | 12.8728 | 62.4031 | 0.0030 |
| CLUTCH + SEASONMID + SEASONLATE | | | | | |
| Intercept | 148.5100 | 33.2839 | 82.2577 | 214.7600 | <0.0001 |
| CLUTCH | 1.5985 | 2.4078 | -3.1316 | 6.3287 | 0.5070 |
| SEASONMID | 47.6873 | 13.4910 | 21.1840 | 74.1907 | 0.0004 |
| SEASONLATE | 38.5252 | 12.6753 | 13.6242 | 63.4262 | 0.0025 |
| CLUTCH + POIMID + POILATE | | | | | |
| Intercept | 236.8600 | 29.6058 | 177.9300 | 295.7900 | <0.0001 |
| CLUTCH | -1.9258 | 2.3242 | -6.4918 | 2.6401 | 0.4077 |
| POIMID | -19.7112 | 9.2703 | -37.9229 | -1.4995 | 0.0339 |
| POILATE | -27.9017 | 11.0494 | -49.6086 | -6.1949 | 0.0119 |
| CLUTCH + SEX + AGE + SEASONMID + SEASONLATE | | | | | |
| Intercept | 163.5600 | 34.4889 | 94.8947 | 232.2200 | <0.0001 |
| CLUTCH | 1.3393 | 2.3932 | -3.3622 | 6.0409 | 0.5760 |
| SEX | -15.6431 | 11.4670 | -38.1704 | 6.8841 | 0.1731 |
| AGE | -6.4974 | 12.8596 | -31.7606 | 18.7658 | 0.6136 |
| SEASONMID | 45.4582 | 13.4977 | 18.9414 | 71.9750 | 0.0008 |
| SEASONLATE | 37.9279 | 0.6084 | 13.1582 | 62.6976 | 0.0028 |

Table 3.3 continued.

| Parameter | Estimate | SE | 95% CI Lower | 95% CI Upper | P-value |
|---|---|---|---|---|---|
| CLUTCH + SEX + POIMID + POILATE | | | | | |
| Intercept | 249.6800 | 30.5412 | 188.8900 | 310.4700 | <0.0001 |
| CLUTCH | -2.1831 | 2.3094 | -6.7199 | 2.3537 | 0.3449 |
| SEX | -18.0252 | 11.8803 | -41.3645 | 5.3142 | 0.1298 |
| POIMID | -19.1477 | 9.2543 | -37.3281 | -0.9673 | 0.0390 |
| POILATE | -26.7431 | 11.0445 | -48.4405 | -5.0457 | 0.0158 |
| CLUTCH + AGE + POIMID + POILATE | | | | | |
| Intercept | 239.4600 | 29.6246 | 180.4800 | 298.4400 | <0.0001 |
| CLUTCH | -1.8099 | 2.3164 | -6.3607 | 2.7408 | 0.4350 |
| AGE | -11.3969 | 13.4086 | -37.7384 | 14.9446 | 0.3957 |
| POIMID | -20.0338 | 9.2664 | -38.2378 | -1.8297 | 0.0311 |
| POILATE | -28.4875 | 11.0527 | -50.2008 | -6.7743 | 0.0102 |
| AGE + POIMID + POILATE + SEX + CLUTCH | | | | | |
| Intercept | 251.5700 | 30.5400 | 190.7700 | 312.3700 | <0.0001 |
| AGE | -10.1163 | 13.3315 | -36.3066 | 16.0740 | 0.4483 |
| POIMID | -19.4507 | 9.2538 | -37.6302 | -1.2712 | 0.0360 |
| POILATE | -27.3011 | 11.0546 | -49.0182 | -5.5840 | 0.0138 |
| SEX | -17.4186 | 11.8685 | -40.7347 | 5.8976 | 0.1428 |
| CLUTCH | -2.0727 | 2.3054 | -6.6018 | 2.4564 | 0.3690 |

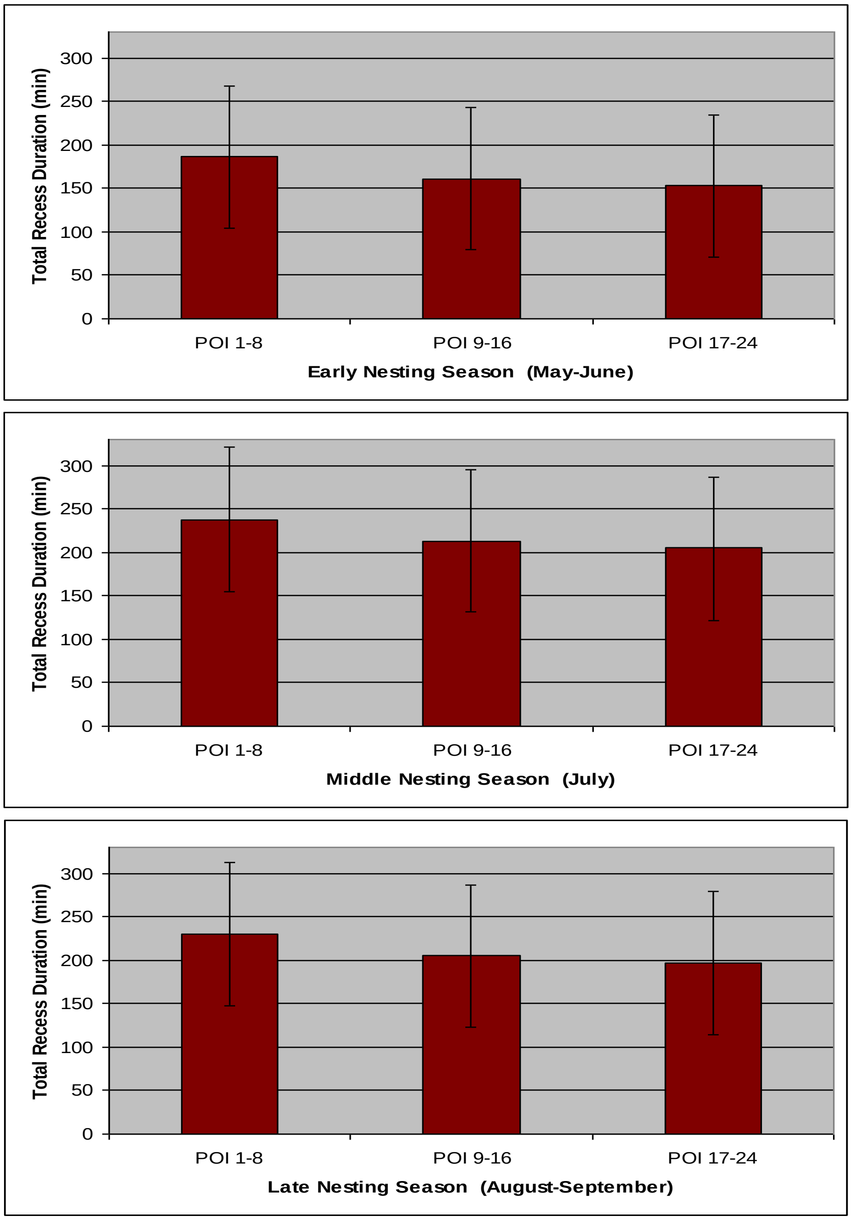

Figure 3.3. Predicted relationship between period of incubation (POI) and nesting season progression (SEASON) with 95% CI on daily nest recess length among northern bobwhites (*Colinus virginianus*) on 3 plantations in southern Georgia and northern Florida, 1999-2006. Data values reflect the mean fixed 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 (SE=.32) eggs.

bobwhites most frequently took one recess per day in the same region as our study. Our findings were similar; we only observed 4 days with more than 2 recess events. As expected with repeated observations on an individual, recess characteristics on one day frequently seemed to influence the bobwhite's behavior the following day. For instance, we noted a trend within birds toward earlier recess initiation following days in which 0 recesses were taken. If attendance is constrained by energy expenditure and reserve depletion, then body reserves following long bouts of attendance likely fall to a minimum level required for incubation (Chaurand and Weimerskirch 1994, Cresswell et al. 2003). The bird is then required to leave the nest earlier than normal to forage and replenish body reserves to another set level (Cresswell et al. 2004).

Although the total amount of time spent in recess was not different between the sexes, males consistently initiated 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 the mid-late afternoon. Interestingly, afternoon foraging trips coincide with the time of day in which most predators were less active and during which we observed the fewest nest depredations (see Chapter II). Furthermore, afternoon ambient temperatures in our study region are similar to the 30° C temperature of incubated bobwhite eggs (Guthery et al 2005). Therefore, foraging during this time may have less impact on egg development and require less energy to reheat the egg. Guthery et al. (2005) also found the majority of afternoon recesses were associated with declining temperatures, but suggest that bobwhites defend eggs more vigorously against hyperthermia than hypothermia and the presence of an incubating parent during the hottest part of the day may actually serve to cool the clutch.

**Recess Duration**

Although the mean daily recess length of successful and unsuccessful nests was not statistically different, likely due to a great deal of variation among birds, the biological ramifications merit consideration. We noted that mean daily recess lengths for failed nests averaged 42 minutes longer/day than recess lengths at successful nests. When extrapolated across the entire 23-day incubation period, the parent was present at the nest for approximately 16 more hours of incubation at successful nests than failed nests. Because higher rates of attentiveness may influence hatching success, and lower rates may expose eggs to temperature stress and predation (Yorio and Dee Boersma 1994), this variation in daily attendance represents a great investment differential that may affect nest success.

*Recess duration and period of incubation*. - Mixed model analysis of our data suggested that period of incubation (clutch age) had a negative effect on recess length. As incubation progressed, we found bobwhites spent less time in recess (thus, more time on the nest) in middle and late incubation compared to early. An increase in investment throughout incubation has previously been noted in bobwhites, especially relevant to a reluctance to abandon a nest in late incubation (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.

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 hormonal cycles.

*Recess duration and nesting season progression.* - We observed an overall increase in recess length across the middle and late nesting seasons relevant to early. Bobwhites are persistent renesters and may nest several times each season (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 throughout the season and could possibly have 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(s) were destroyed 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 better 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 rain 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.

Finally, as late season approaches the bobwhite may have already successfully hatched a brood and may be attempting to renest. In this situation, a late season nest may not be worth further physical decline if successful reproduction for the season has already been achieved.

*Miscellaneous behavioral observations.* - The tendency of the non-incubating bobwhite mate to avoid the nest site is well documented (Stoddard 1931). We viewed thousands of incubation hours of 118 birds and very rarely observed 2 bobwhites in camera view at the same time. However, a nest located on Tall Timbers in June of 2001 was an exception. We observed 2 bobwhites in camera view at the nest on 3 different days (June 7, 9, and 10). These events occurred as the incubating female returned from recess, presumably accompanied by its mate. Both birds were in camera view at the same time.

On June 9, the pair returned to the nest and the female entered the nest bowl to resume incubation. The male stood near the nest and entered the nest bowl with the female for a brief period before exiting the nest and leaving camera view. This was the only time we noted 2 bobwhites in the nest bowl at the same time.

## Conclusions

We found the progression of incubation and nesting season most influenced patterns of bobwhite nest recess and attendance. We observed little difference between the sexes, but recess length at failed nests was longer than at successful nests. We feel this discrepancy in attentiveness may be biologically important.

Although the trends revealed by our data were clear, a great deal of variation existed both within and among the birds in our sample. Additionally, the comprehensive effects of external factors such as climate, geographic location, habitat quality, predator context, and density on bobwhite recess and attendance patterns are unknown. Therefore, our results may not be representative of bobwhite behavior in other regions. We propose further research of this type in other locales to obtain a more thorough understanding of the factors influencing bobwhite investment.

## LITERATURE CITED

Afton, A.D. 1980. Factors affecting incubation rhythms of northern shovelers. Condor 82:132-137.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* Proceedings of Second International Symposium on Information Theory. B.N Petrov and F. Csaki, editors. Akademiai Kiado, Budapest, Hungary.

American Ornithologists' Union. 1988. Report of committee on use of wild birds in research. Auk 105 (1, Supplemental): 1-41.

Barash, D.P. 1975. Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. Wilson Bulletin 87:367-373.

Brennan, L.A. 1999. Northern bobwhite *Colinus virginianus.* In the Birds of North America No. 397. A. Poole and F. Gill, editors. The Birds of North America, Inc., Philadelphia, PA, USA.

Bryan, S.M. and D.M. Bryant. 1999. Heating nest boxes reveals an energetic constraint on incubation behavior in great tits, *Parus major*. Proceedings: Biological Sciences 266:157-162.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and inference: an information-theoretic approach. Springer-Verlag, New York, NY.

Chaurand, T. and H. Weimerskirch. 1994. Incubation routine, body-mass regulation and egg neglect in the blue petrel (*Halobaena caerulea*). Ibis 136:285-290.

Church, K.E., J.R. Sauer, and S. Droege. 1993. Population trends of quails in North America. Proceedings of the National Quail Symposium 3:44-54.

Cresswell, W., S. Holt, J.M. Reid, D.P. Whitfield, R.J. Mellanby. 2003. Do the energetic demands of incubation constrain incuation scheduling in a biparental species? Behavioral Ecology 14:97-102.

Cresswell, W., S. Holt, J.M. Reid, D.P. Whitfield, R.J. Mellanby, D. Norton, and S. Waldron. 2004. The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. Behavioral Ecology 15:498-507.

Flint, P.L., and J.B. Grand. 1999. Incubation behavior of spectacled eiders on the Yukon-Kuskokwim Delta, Alaska. Condor 101:413-416.

Gloutney, M.L., R.T. Alisauskas, A.D. Afton, and S.M. Slattery. 2004. Foraging time and dietary intake by breeding Ross's and lesser snow geese. Oecologia 127:78-86.

Goldsmith, A.R. 1982. Plasma concentrations of prolactin during incubation and parental feeding throughout repeated breeding cycles in canaries (*Serinus canarius*). Journal of Endocrinology 94:51-59.

Guthery, F.S. 1997. A philosophy of habitat management for northern bobwhites. Journal of Wildlife Management 61:291-301.

Guthery, F.S,, A.R. Rybak, S.D. Fuhlendorf, T.L. Hiller, and S.G. Smith. 2005. Aspects of the thermal ecology of bobwhites in north Texas. Wildlife Monographs 159:1–36.

Hall, M.R. 1987. External stimuli affecting incubation behavior and prolactin secretion in the duck (*Anas platyrhynchos*). Hormones and Behavior 21:269-287.

Hanssen, S.A., H. Engebretsen, K.E. Erikstad. 2002. Incubation start and egg size in relation to body reserves in the common eider. Behavioral Ecology and Sociobiology 52:282-288.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Jonsson, J.E., A.D. Afton, R.T. Alisauskas, C.K. Bluhm, and M.E. El Halawani. 2006. Ecological and physiological factors affecting brood patch area and prolactin levels in arctic-nesting geese. Auk 123:405-418.

Lorenz, N.F. 2005. Environmental factors influencing incubation constancy and recess frequency in gadwall (*Anas strepera*) in the prairie pothole region of North Dakota. M.S. Thesis, Louisiana State University, Baton Rouge.

MacCluskie, M.C. and J.S. Sedinger. 1999. Incubation behavior of northern shovelers in the subarctic: a contrast to the prairies. Condor 101:417-421.

Moller. A.P. 1991. Double broodedness and mixed reproductive strategies by female swallows. Animal Behaviour 42:671-679.

Monaghan, P. and R.G. Nager. 1997. Why don't birds lay more eggs? Trends in Ecology and Evolution 12:270-274.

Persson, I. and G. Göransson. 1999. Nest attendance during egg laying in pheasants. Animal Behaviour 58:159-164.

Rauter, C., and H. Reyer. 1997. Incubation pattern and foraging effort in the female water pipit *Anthus spinoletta*. Ibis 139:441-446.

Rosene, W. 1969. The bobwhite quail: its life and management. Rutgers University Press, New Brunswick, New Jersey.

Rytkonen, S., M. Orell, and K. Koivula. 1995. Pseudo concorde fallacy in the willow tit? Animal Behaviour 49:1017-1028.

SAS Institute. 2003. SAS/STAT software, version 9.1. SAS Institute, Cary, North Carolina, USA.

Skutch, A.F. 1976. Parent birds and their young. University of Texas Press, Austin.

Smith, H.D., F.A. Stormer and R.D. Godfrey, Jr. 1981. A collapsible quail trap. Rocky Mountain Forest and Range Experiment Station. Research Note RM-400. 3 pp.

Staller, E.L., W.E. Palmer, J.P. Carroll, R.P. Thornton, and D.C. Sisson. 2005. Identifying predators at northern bobwhite nests. Journal of Wildlife Management 69:124-132.

Stanford, J.A. 1972. Second broods in bobwhite quail. Proceedings of the National Bobwhite Quail Symposium 1:199-204.

Stearns, S.C. 1992. The evolution of life histories. Oxford: Oxford University Press.

Stoddard, H.L. 1931. The bobwhite quail: its life history and management. Charles Scribner's Sons, New York, USA.

Thornton, R. 2003. The experimental effect of mesomammal predator removal on depredation of northern bobwhite in south Georgia and north Florida. M.S. Thesis, University of Georgia, Athens.

Trivers, R.L. 1972. Parental investment and sexual selection. Pp. 136-179 *in* B. Campbell, Editor. Sexual Selection and the Descent of Man. Chicago: Aldine.

Van Roo, B.L., E.D. Ketterson, and P.J. Sharp. 2003. Testosterone and prolactin in two songbirds that differ in parental care: the blue-headed vireo and the red-eyed vireo. Hormones and Behavior 44:435-441.

Weathers, W.W. and K.A. Sullivan. 1989. Nest attentiveness and egg temperature in the yellow-eyed junco. Condor 91:628-633.

White, C.G. and R.A. Garrott. 1990. Analysis of radio-tracking data. Academic Press, San Diego, CA. 383 pp.

Williams, C.K., F.S. Guthery, R.D. Applegate, and M.J. Peterson. 2004. The northern bobwhite decline: scaling our management for the twenty-first century. Wildlife Society Bulletin 32:861-869.

Yorio, P. and P.D. Boersma. Consequences of nest desertion and inattendance for magellanic penguin hatching success. Auk 111:215-218.

Appendix 3A. Number of 0, 1, 2, and total nest recesses taken by nesting season and incubation stage by male and female northern bobwhites (*Colinus virginianus*) on 3 plantations 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 |

Appendix 3B. Predicted nest recess length, standard error for the prediction (SE), and 95% confidence interval for nest recesses taken in combinations of: period of incubation and stage of the nesting season by male and female northern bobwhites (*Colinus virginianus*) on 3 plantations in southern Georgia and northern Florida, 1999 – 2006. Recess length generally decreased throughout incubation and increased as the nesting season progressed relative to the early season.

| Temporal Categories | Predicted Recess Length (min) | SE for Predicted | 95% Confidence Interval | |
|---|---|---|---|---|
| | | | Lower | Upper |
| **Early Season** | | | | |
| Early Incubation | 186.10 | 41.83 | 103.91 | 268.28 |
| Middle Incubation | 161.04 | 41.71 | 79.10 | 243.00 |
| Late Incubation | 153.06 | 41.92 | 70.71 | 235.40 |
| **Middle Season** | | | | |
| Early Incubaton | 237.89 | 42.14 | 155.11 | 320.67 |
| Middle Incubation | 212.84 | 41.76 | 130.79 | 294.89 |
| Late Incubation | 204.85 | 41.98 | 122.38 | 287.33 |
| **Late Season** | | | | |
| Early Incubation | 229.86 | 41.97 | 147.40 | 312.32 |
| Middle Incubation | 204.80 | 41.48 | 123.33 | 286.29 |
| Late Incubation | 196.82 | 41.71 | 114.87 | 278.77 |

# CHAPTER 4

# CONCLUSIONS AND FUTURE RESEARCH NEEDS

The behavioral ecology of nesting northern bobwhites (*Colinus virginianus*; hereafter bobwhite) is poorly understood. As in other birds (Brown et al. 1998), the spatial and temporal dispersion of nests and the bobwhite's cryptic coloration historically made it difficult to locate nests and directly monitor nest behavior. The advent of continuous-recording, near-infrared cameras allowed us to directly monitor bobwhite nests throughout incubation. As a result, we were able to continuously and directly observe incubation behaviors rather than drawing conclusions obtained from brief "snapshots" of nest observation.

As predicted in the literature (Trivers 1972, Moller 1991, Rauter and Reyer 1997), we found investment behaviors to be influenced by a multitude of factors including sex of parent, incubation stage, and point in the nesting season. We found little difference in nesting behavior between juvenile and adult bobwhites or according to clutch size.

With regards to nest defense, predator species was the most important factor influencing the likelihood of defense. Bobwhites were reluctant to defend against meso-mammal species that were capable of killing an adult bird. Rather, defense was initiated against species that predominantly posed a risk to the nest, such as armadillos (*Dasypus novemcinctus*), snakes (particularly *Elaphus spp.* and *Lampropeltis getulus*), fire ants (*Solenopsis spp.*), and fox squirrels (*Sciurus niger*). Successful nest defense events among bobwhites were infrequent, but did occur. Without video documentation, identifying such events would be nearly impossible; a hatched nest by default leaves little sign of a successful defense. Furthermore, any defensive attempt at a failed nest would necessarily be unsuccessful. Among successful defenses, all but one was aggressively initiated by the bobwhite before the predator gained access to the nest bowl. In each case, the predators seemed startled by the bobwhite and were likely never aware of the nest. Conversely, defensive attempts initiated after the predator reached the nest were typically unsuccessful.

Nest recess frequency and duration were most influenced by period of incubation and stage of the nesting season. As incubation progressed, recess length decreased. Thus, as the clutch approached hatching, the bobwhite invested more in the nest by increasing nest attentiveness. The increasing value of an aging clutch (Barash 1975), and the increasing cost of replacing that clutch may play a role in the elevated rates of nest constancy we observed among bobwhites during late incubation.

As the nesting season progressed, we saw an increase in recess length and a resulting decrease in attendance. We predict this is primarily due to declining physical condition among incubating bobwhites. Because bobwhites are persistent renesters, late season birds have likely attempted several nests and may be forced to spend more time foraging to maintain body reserves at a level required for incubation. Additionally, environmental stresses in late season may require bobwhites to forage longer than in early season to achieve the same food intake.

## FURTHER RESEARCH

Though the trends revealed by our data were clear, a great deal of variation exists both within and among the birds in our sample. Additionally, the comprehensive effects of external factors such as climate, geographic location, habitat quality, predator context, and density on bobwhite recess and attendance patterns are unknown. Therefore, our results may not be representative of bobwhite behavior in other regions. We propose further research of this type in other locales to obtain a more thorough understanding of the factors influencing bobwhite investment.

The relationship between body condition and incubation rhythms in bobwhites also warrants further study. A large body of work on other avian species suggests parental body condition entering incubation influences attentiveness and investment (Persson and Göransson 1999, Cresswell et al. 2004). This relationship may have management implications if habitat quality and/or supplemental feeding positively influence body condition and nesting success.

The hormonal ecology of nesting bobwhites is another area in which further research is needed. Prolactin and testosterone have been shown to be important influences affecting avian incubation and investment (Hall 1987, Jonsson et al. 2006), but their effects have yet to be fully evaluated in bobwhites or other upland gamebirds. Hormonal research would be difficult to conduct on wild bobwhites, but similar studies on waterfowl and passerine species could provide a framework for a manipulative experimental design.

Whereas video cameras have proven useful for monitoring a variety of wildlife species (Cutler and Swann 1999), future bobwhite incubation research should also employ the use of temperature data loggers or thermal radiotransmitters in nests (Guthery et al. 2005, Voss et al. 2006). Their implementation would allow for more time efficient analysis of attendance patterns and would also allow researchers to further evaluate the relationship between temperature and incubation behavior.

## LITERATURE CITED

Barash, D.P. 1975. Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. Wilson Bulletin 87:367-373.

Brown, K.P., H. Moller, J. Innes, and P. Jansen. 1998. Identifying predators at nests of small birds in a New Zealand forest. Ibis 140:272-279.

Cresswell, W., S. Holt, J.M. Reid, D.P. Whitfield, R.J. Mellanby, D. Norton, and S. Waldron. 2004. The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. Behavioral Ecology 15:498-507.

Cutler, T.L. and D.E. Swann. 1999. Using remote photography in wildlife ecology: a review. Wildlife Society Bulletin 27:571-581.

Guthery, F.S,, A.R. Rybak, S.D. Fuhlendorf, T.L. Hiller, and S.G. Smith. 2005. Aspects of the thermal ecology of bobwhites in north Texas. Wildlife Monographs 159:1-36.

Hall, M.R. 1987. External stimuli affecting incubation behavior and prolactin secretion in the duck (*Anas platyrhynchos*). Hormones and Behavior 21:269-287.

Jonsson, J.E., A.D. Afton, R.T. Alisauskas, C.K. Bluhm, and M.E. El Halawani. 2006. Ecological and physiological factors affecting brood patch area and prolactin levels in arctic-nesting geese. Auk 123:405-418.

Moller. A.P. 1991. Double broodedness and mixed reproductive strategies by female swallows. Animal Behavior 42:671-679.

Persson, I. and G. Göransson. 1999. Nest attendance during egg laying in pheasants. Animal Behaviour 58: 159-164.

Rauter, C., and H. Reyer. 1997. Incubation pattern and foraging effort in the female water pipit *Anthus spinoletta*. Ibis 139:441-446.

Trivers, R.L. 1972. Parental investment and sexual selection. Pp. 136-179 *in* B. Campbell, Editor. Sexual Selection and the Descent of Man. Chicago: Aldine.

Voss, M.A., F.R. Hainsworth, and S.N. Ellis-Felege. 2006. Use of a new model to quantify compromises between embryo development and parental self-maintenance in three species of intermittently incubating passerines. Journal of Thermal Biology 31:453-460.