PATTERNS OF NEST ATTENDANCE IN FEMALE WOOD DUCKS[1]

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Abstract. We examined sources of variation in incubation patterns among female Wood Ducks (*Aix sponsa*), and investigated the effect of female nest attentiveness on incubation period. Data were collected from 44 females ($n = 911$ days) using temperature data loggers to monitor nest attendance throughout incubation. Mean ($\pm$ SE) incubation constancy was $86.9 \pm 0.6\%$ and incubation period averaged 30.9 ± 0.2 days. Females took an average of two bimodally-distributed recesses per day. Duration of recesses averaged 98.6 ± 3.4 min, but were shorter in the morning than in mid-day or late afternoon. Body mass of incubating females declined 0.68 ± 0.2 g day^{-1}, but there was no relationship between constancy and early incubation body mass or weight change of females. Incubation constancy was not correlated with length of the incubation period. For most females, incubation constancy and recess frequency did not change as incubation progressed. The fact that incubating females only lost an average of 3% of body mass, and constancy was not related to either body mass or length of the incubation period, suggests that females were not constrained energetically. Finally, we propose that the combination of reduced predation risk and the need of neonates to be more functionally mature at hatching has selected for longer incubation periods in Wood Ducks and other cavity-nesting waterfowl.

Key words: Aix sponsa, Anatidae, body mass, Cairinini, incubation behavior, incubation period, Wood Duck.

INTRODUCTION

Patterns of nest attendance during incubation vary widely among North American waterfowl. Differences in body size among species account for part of this variation (Afton and Paulus 1992). Females of large-bodied geese (Anserinae), for example, rely on nutrient reserves during the incubation period, and spend more time on nests than small-bodied ducks (Anatinae) that rely more on exogenous resources to meet their energetic requirements (Raveling 1979, Krapu 1981, Drobney 1982). This pattern also is true within ducks. Incubation constancies of Mallards (89%; *Anas platyrhynchos*) and Canvasbacks (87%; *Aythya valisineria*) are greater than smaller species like Green-winged Teal (79%; *Anas crecca carolinensis*) (Afton 1978, Gatti 1983, Meade 1996). Incubation behaviors also may vary with weather, body condition, and day of incubation (Afton and Paulus 1992), but only recently have investigators tested whether individual females varied in their response to these

factors (Mallory and Weatherhead 1993, Flint and Grand 1999, MacCluskie and Sedinger 1999).

Incubation behaviors of Wood Ducks (*Aix sponsa*) and sources of variation in these patterns have not been adequately studied (Afton and Paulus 1992). Wilson and Verbeek (1995) measured temperatures of Wood Duck nests and showed that nest temperatures increased as incubation progressed, but could not attribute this pattern to increasing nest attentiveness by incubating females. We initiated this study to document patterns of incubation, investigate variation in incubation rhythms among females relative to day of incubation and female body mass, and examine the effect of incubation constancy on incubation period. We predicted that incubation constancy would increase with female body mass (Afton and Paulus 1992), and that more attentive females would have shorter incubation periods. In several species of ducks, incubation constancy declines as the incubation period progresses, possibly in response to increasing ambient temperature (Mallory and Weatherhead 1993), increasing embryonic heat (Drent 1970), or energetic constraints on females (Afton and Paulus 1992); therefore, we also predicted that females would spend more time off the nest as incubation proceeded.

METHODS

Breeding Wood Ducks were studied in 1996 and 1997 on Eufaula National Wildlife Refuge (NWR) in southwestern Georgia (32°N, 85°W). Eufaula NWR is centered on Lake Eufaula, an impoundment of the Chattahoochee River. The study area was described in detail by Moorman and Baldassarre (1988).

During the breeding season (January–July), nest boxes (n = 43 in 1996, n = 38 in 1997) were checked weekly to monitor nesting activity. Date of nest initiation was estimated by subtracting the number of eggs in the nest when it was first found from the Julian date that the nest box was checked (Hepp et al. 1990). Because brood parasitism is common in Wood Ducks, if the number of eggs was greater than the number of days between nest-box checks, we assumed these nests were initiated on the day immediately following the last nest check. Day of incubation was determined by candling eggs (Hanson 1954). Females were captured in early incubation (≤ day 10) and anesthetized using methoxyflurane to help reduce nest abandonment (Rotella and Ratti 1990). Females were weighed with a Pesola spring scale to the nearest 5 g, banded with a U.S. Fish and Wildlife Service leg band, and aged as yearling or adult using methods of Harvey et al. (1989). Females were recaptured and weighed again in late incubation (≥ day 25).

Incubation constancy and attendance patterns were determined with temperature data loggers installed in nests during late egg-laying or early incubation by first removing contents of the nest and installing a platform containing a single wooden egg in the nest box. A thermistor probe was embedded in each wooden egg, and wooden eggs were securely fastened to each platform with lag bolts (10 cm) to prevent females from moving them. The tip of the thermistor was exposed on top of the egg to ensure contact with the brood patch of the incubating female, and a cable (61 cm) connected the thermistor to the data logger. Wood chips and eggs were returned to the box after installing the platform. Wooden eggs were positioned in the center of the clutch, and data loggers were placed beneath wood chips. Data loggers were programmed to record nest temperatures every 6.4 min for 35 days. Data loggers were retrieved, and data were down-loaded after ducklings hatched and exited the nest box.

Temperature data for each female were visually scrutinized both as plotted data and on spreadsheets. A rise or drop in temperature of 2.0°C was considered movement on or off the nest by the female. We validated this assumption by recording actual times that females were observed leaving or returning to nests, and comparing these values to arrival and departure times estimated from the data loggers. Data from 40 nests in which females were flushed, were captured and removed, or were naturally returning to or leaving nests were used for the validation. Differences (minutes) between actual and estimated times were calculated. The magnitude of these differences did not vary monthly ($F_{4, 111}$ = 1.29, P = 0.28) or among females that flushed, were captured, or were taking natural recesses ($F_{2, 111}$ = 0.63, P = 0.53), so we pooled data. The difference between actual and estimated times that females departed or returned to nests averaged 2.8 ± 0.3 min (n = 118), and 93% of estimates were within 6 min of the actual time recorded in the field. Using the criterion of a 2.0°C temperature change, therefore, provided an accurate assessment of when incubating females were on and off the nest. If the rise or drop of 2.0°C was not maintained for two successive time periods (elapsed time = 13 min), then we considered the female to be involved in a comfort movement within the nest box. Daily incubation constancy was the percentage of time spent on the nest during a 24-hr period beginning at midnight. Overall incubation constancy was the average of the daily incubation constancies and was calculated for each female. Recesses were periods of time spent off the nest (Skutch 1962). Averages of recess frequency and duration were calculated for each female. Only data from complete 24-hr periods were used to calculate incubation constancy, recess frequency, and recess duration. Incubation period was the number of days from the onset of incubation to hatching. Data loggers revealed the date that ducklings exited the nest box, and hatch date was assumed to be the previous day.

STATISTICAL ANALYSIS

We restricted analyses of incubation rhythms to the period from day 2 to 32 (n = 6–40 females day^{-1}) because sample sizes on other days were small (≤ 3 females). Constancy (%) was arcsine
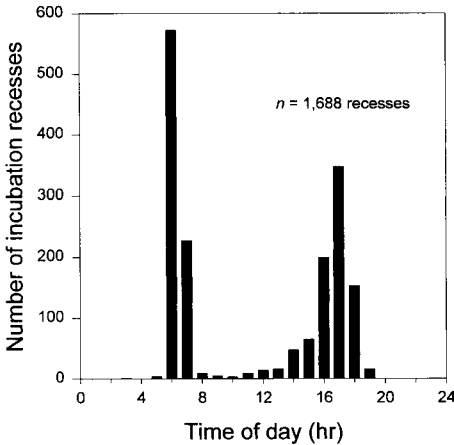
FIGURE 1.   Distribution of recess initiation times for female Wood Ducks (n = 44) at Eufaula National Wildlife Refuge, Georgia, 1996–1997. Time of day is represented as 24 1-hr time blocks, beginning at midnight (0).

transformed before analysis to help meet the assumption of normality. We examined variation in daily incubation constancy and recess frequency using ANCOVA with female as a class variable, day of incubation as the covariate, and the interaction of female and day of incubation. This analysis allowed us to test for among-female variation in incubation behavior (Flint and Grand 1999, MacCluskie and Sedinger 1999). We sampled 6 females in both years, so levels of among-female variation may be conservative. We used simple correlation analysis to test whether date of nest initiation and overall incubation constancy were related to early incubation body mass of females and changes in body mass during incubation. A partial correlation that controlled for variation in nesting date was used to test the relationship between con-

TABLE 1.   Recess duration (min) of female Wood Ducks in relation to time of day at the Eufaula National Wildlife Refuge, Georgia, 1996–1997. No recesses occurred between 20:01–02:00. Means with different letters are significantly different (P < 0.05).

Recess duration	n	Mean ± SE	Range
Morning (02:01–08:00)	44	86.6 ± 3.4 A	42.5–139.4
Mid-day (08:01–14:00)	20	104.3 ± 7.6 B	38.0–168.9
Afternoon (14:01–20:00)	44	114.2 ± 3.9 B	60.6–169.2

stancy and incubation period. We used one-way ANOVA to test whether duration of recesses varied with period of the day (morning, 02:01–08:00; mid-day, 08:01–14:00; afternoon, 14:01–20:00) followed by Tukey's test to separate mean values. Statistical analyses were completed with SAS (SAS Institute 1988). All means are reported ± SE.

RESULTS

Data were collected from 44 female Wood Ducks (n = 911 days). Females spent 86.9 ± 0.6% (range = 78.1–93.2%) of the day incubating, and the incubation period averaged 30.9 ± 0.2 days (range = 28–34 days). The relationship between incubation constancy and day of incubation varied among females ($F_{43,823}$ = 6.1, P < 0.001). Incubation constancy did not change for most (52%) females as incubation progressed, but constancy for others increased (32%) or declined (16%) with day of incubation. Females that initiated nests early in the season were heavier (r = −0.60, n = 44, P < 0.001) and lost weight more rapidly (r = 0.50, n = 39, P < 0.001) during incubation than females that nested later. Body mass of incubating females declined an average of 0.7 ± 0.2 g day^{-1}, but body mass of 38.5% (15 of 39) of females did not decrease. There was no relationship between overall incubation constancy and either early incubation body mass (r = 0.17, n = 44, P = 0.27) or weight change of females (r = 0.13, n = 39, P = 0.44). Incubation constancy also was not correlated with length of the incubation period (r = −0.08, n = 41, P = 0.61), after controlling for variation in clutch size.

Females took an average of 1.86 ± 0.04 recesses day^{-1}, and the distribution of recesses was bimodal (Fig. 1). Most (73.8%) daily incubation bouts (n = 911) were characterized by a morning and an afternoon recess; single recesses, either in the morning (10.1%) or in the afternoon (9.9%), comprised most remaining bouts. The relationship between recess frequency and day of incubation varied among females ($F_{43,823}$ = 4.5, P < 0.001). Frequency of recesses did not change as incubation progressed for most (68%) females, but recess frequency for others either declined (21%) or increased (11%). Duration of recesses averaged 98.6 ± 3.4 min, but were shorter in the morning than in mid-day or late afternoon ($F_{2,105}$ = 12.3, P < 0.001; Table 1).

DISCUSSION

INCUBATION CONSTANCY

Incubation constancy of Wood Ducks was similar to that of other cavity-nesting ducks such as Hooded Mergansers (*Lophodytes cucullatus*; Mallory et al. 1993) and Common Goldeneyes (*Bucephala clangula*; Mallory and Weatherhead 1993, Zicus et al. 1995), as well as ground-nesting species of comparable body mass (Afton and Paulus 1992). However, incubation constancy varies greatly within species. Intraspecific variation in attendance patterns has been attributed to factors such as habitat quality (Zicus et al. 1995) and female body condition (Aldrich and Raveling 1983, Gatti 1983). In Wood Ducks, we found no indication that body mass at the start of incubation or rate of weight change during incubation were related to incubation constancy.

For incubating birds there is a trade-off between maintaining good body condition and caring for developing eggs. Incubating females face energetic constraints and may abandon nests if weight loss becomes too great (Mallory and Weatherhead 1993). In some years, female Wood Ducks that finished incubation with low body mass had lower survival (Hepp et al. 1990) and were less likely to have second broods (Kennamer and Hepp 1987) than females in better condition. More foraging time may help females meet energetic demands, but increased time away from nests also can be harmful. In small-bodied species, presence of females at the nest probably does not reduce predation as it does for large-bodied species (Thompson and Raveling 1987, Swennen et al. 1993), but reduced constancy can lead to longer incubation periods and, hence, increased exposure of nests to predators (Zicus et al. 1995).

In this study, incubation constancy of Wood Ducks was not related to female body mass or length of the incubation period, indicating that incubating females were not energetically constrained. Similar results have been reported for Spectacled Eiders (*Somateria fischeri*) in Alaska (Flint and Grand 1999). Body mass of females at Eufaula NWR declined approximately 3% during incubation, but body mass of more than one-third of females did not decrease. During a 3-year study of incubating Wood Ducks in South Carolina, body mass declined an average of 2–7%, and only when weight loss was highest did females that were relatively light at the end of incubation have lower probabilities of surviving to the next breeding season than heavy females (Hepp et al. 1990). Constraints on incubating females in South Carolina, therefore, were not apparent until declines in body mass averaged >5%, which is well above that of Wood Ducks nesting at Eufaula NWR and supports our contention that these females were not constrained during incubation.

Small-bodied waterfowl rely heavily on exogenous nutrients to meet energetic demands of incubation (Afton and Paulus 1992). Female Wood Ducks incubating early in the season were heavier and lost mass at a faster rate than females nesting later (Harvey et al. 1989, Hepp et al. 1990, this study). Larger energy reserves are potentially important to females that begin incubation early in the season, because thermoregulatory costs are greater and environmental conditions affecting food availability may be more unpredictable. Heavy, early-nesting females, for example, were able to incubate nests with the same constancy as smaller females that nested later.

INCUBATION PERIOD

High levels of incubation constancy may result in shorter incubation periods which would be advantageous by reducing exposure of nests to predation and giving females a greater chance of renesting. The relationship between constancy and incubation period, however, varies among waterfowl. Eichholz and Sedinger (1998) found no relationship between incubation constancy and incubation period for Black Brant (*Branta bernicla*), but others have reported that greater constancy resulted in reduced incubation periods (Aldrich and Raveling 1983, Zicus et al. 1995). We found no relationship between overall incubation constancy and incubation period in Wood Ducks, suggesting that other factors are important in determining length of incubation. If strong female-effects exist in development time as MacCluskie et al. (1997) found in Mallards, then finding a relationship between constancy and incubation period may be difficult.

Average incubation constancy of open-nesting ducks (84.8%) is similar to that of cavity-nesting species (84.4%), but open-nesting ducks have incubation periods that average about 6 days shorter than cavity-nesters (Afton and Paulus 1992). Most selective forces acting on incubation period favor rapid embryonic development

and short incubation periods (Ricklefs and Starck 1998). Nest predation can exert considerable selection pressure on clutch size in waterfowl (Arnold et al. 1987), and it is possible that predation risk also has influenced incubation period. Nest success of Wood Ducks using natural cavities is high (40–64%; Bellrose and Holm 1994, Ryan et al. 1998). In contrast, nest success of ground-nesting ducks in the Prairie Pothole Region of the U.S. and Canada is often less than 15–20%, and predation accounts for more than 70% of nest failures (Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995). Short incubation periods, therefore, would be an obvious advantage to prairie-nesting ducks.

Predation risk may be lower for cavity-nesting species, but benefits of short incubation periods also should exist. Shorter incubation periods in Wood Ducks may increase chances of renesting and producing a second brood (Kennamer and Hepp 1987, Moorman and Baldassarre 1988). At northern latitudes, shorter incubation periods would give cavity-nesting females more time to raise their broods and prepare for fall migration. It is clear that shorter incubation periods also would be beneficial to cavity-nesting species. Why then do lengthy incubation periods persist?

Differences in embryonic development may help explain variation in incubation periods among birds (Ricklefs and Starck 1998). Embryos of altricial and precocial birds grow at similar rates, but precocial species undergo a longer phase of tissue maturation toward the end of incubation and generally have longer incubation periods (Ricklefs and Starck 1998). The fraction of water in muscle tissue can be used to index functional maturity; low values indicate greater functional maturity (Ricklefs 1983). Functional maturity of Wood Duck neonates (2.7; Clay et al. 1979) is greater than that of neonates of some ground-nesting waterfowl (4.3; Slattery and Alisauskas 1995). A longer period of embryogenesis that results in more functionally mature neonates may be required by cavity-nesting species, so that ducklings can successfully leave the nest. Hooded Merganser (*Lophodytes cucullatus*) and Wood Duck ducklings begin exiting nests using a series of vertical leaps to ascend the cavity wall and then scale the remaining distance (Siegfried et al. 1974, Bellrose and Holm 1994). We propose that the combination of reduced predation risk and the need of neonates to be more functionally mature at hatch has select-ed for longer incubation periods among cavity-nesting waterfowl.

In summary, we observed considerable individual variation in incubation behavior, but incubating females generally were not energetically constrained. Further studies are needed to address sources of variation in incubation rhythms among female Wood Ducks.

ACKNOWLEDGMENTS

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