

INCUBATION BEHAVIOR OF SPECTACLED EIDERS ON THE YUKON-KUSKOKWIM DELTA, ALASKA¹

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Abstract. We studied incubation behavior of Spectacled Eiders (*Somateria fischeri*) on the Yukon-Kuskokwim Delta in 1996. We trapped 19 females on their nests and weighed them in early incubation and again at hatch. Average daily weight loss for incubating females was 16.6 ± 1.0 g day⁻¹, which resulted in a cumulative loss of 26% of body weight throughout incubation. Nest attendance was monitored for a portion of the incubation period using temperature sensing artificial eggs. Incubation constancy averaged $90 \pm 1\%$. Average recess length was 37.1 ± 0.9 min, and nests cooled an average of $4.2 \pm 0.1^\circ\text{C}$ during recesses. Recess frequency averaged 2.5 ± 0.1 recesses day⁻¹, and most recesses (70%) occurred between 10:00 and 22:00. Incubation constancy varied among females, but was not related to changes in body weight or incubation period. There was no influence of ambient temperature on incubation recess length, however most recesses were taken during the warmest part of the day. We found considerable variation among females in patterns of daily incubation constancy, nest cooling, recess frequency, and recess length. It is not clear from our results what factors constrain incubation behavior of Spectacled Eiders, but we suggest that individual females respond to a complex suite of variables.

Key words: incubation behavior, incubation constancy, nest attentiveness, *Somateria fischeri*, Spectacled Eider, weight loss.

Incubating birds face three, sometimes conflicting, selection pressures: maintaining a favorable thermal environment for embryo development, maintaining a favorable energy balance for themselves, and minimizing the risk of predation on themselves and their eggs. Female waterfowl typically rely on stored reserves to meet some of their maintenance requirements during incubation (Afton and Paulus 1992). Afton and Paulus (1992) report a positive relationship between incubation constancy and weight loss among waterfowl species. High incubation constancy allows females to maintain favorable environmental conditions within the nest which favors high egg-hatchability (Afton and Paulus 1992). Additionally, females that are more attentive to the nest may have shorter incubation periods (Aldrich and Raveling 1983, Wilson and Verbeek 1995, Zicus et al. 1995), thereby reducing the exposure

of eggs to predation. Furthermore, Swennen et al. (1993) report that a majority of egg loss in Common Eiders (*Somateria mollissima*) occurs during incubation recesses, and it has been suggested that females time incubation recesses to minimize exposure to predation (Afton 1980, Hohman 1986, Swennen et al. 1993). The combination of these costs to incubating females has led to the suggestion that incubation behavior is the result of trade-offs between loss of body condition, maintenance of egg viability, and risk of predation (Thompson and Raveling 1987, Afton and Paulus 1992).

The goal of this study was to describe the incubation behavior of Spectacled Eiders (*Somateria fischeri*) and to relate the incubation constancy of individuals to changes in body weight and environmental factors. We test hypotheses regarding variation in incubation constancy, and describe variation in incubation constancy in terms of recess frequency and recess length.

METHODS

This study was conducted along the lower Kashunuk River ($61^\circ 20' \text{N}$, $165^\circ 35' \text{W}$) on the coastal fringe of the Yukon Delta National Wildlife Refuge, Alaska in 1996. The study area and nest searching procedures have been described in detail by Grand et al. (1997) and Grand and Flint (1997). We trapped and weighed females on their nests early in incubation and again just prior to hatch. To reduce nest abandonment, we anesthetized females using methoxyflurane (Rotella and Ratti 1990) and placed females near the nest before we left the area. Ambient temperatures ($\pm 0.2^\circ\text{C}$) were recorded hourly at a shaded location adjacent to the study area. We monitored incubation behavior using an artificial egg attached to a single channel data logger as described by Flint and MacCluskie (1995). Artificial eggs were placed in nests at time of first capture; they sampled nest temperature ($\pm 0.2^\circ\text{C}$) every 6.5 min. Nests were visited weekly to download data and reposition artificial eggs. Data recorded on days that observers disturbed females were excluded from analyses.

Nest temperatures during incubation recesses were transformed to actual nest temperatures using the procedure outlined by Flint and MacCluskie (1995). It was apparent based on corrected temperature records that the switches in the artificial eggs did not always function correctly to record nest attendance. Based on periods when the switches worked correctly, we assumed that an incubation recess began anytime the nest temperature declined by $>1^\circ\text{C}$ in two successive temperature records (elapsed time 13 min.) and the recess ended when nest temperature began to increase. Given these criteria, we reanalyzed nest temperature

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records to estimate total time spent on nests and recess characteristics. Incubation constancy was defined as the percentage of all records during which the female was on the nest. Likewise, daily incubation constancy was defined as incubation constancy during a 24-hr period beginning at midnight. Time of day for incubation recesses was defined as the hour in which the recess started. Ambient temperatures for recesses were defined as the average temperature for the hour in which the recess started. Incubation stage (days) was determined from information on egg laying and from candling (Grand and Flint 1997). Although we accept that true incubation starts before the clutch is complete (Afton and Paulus 1992), we defined an index to incubation period as the number of days between the day the last egg was laid and hatch.

STATISTICAL ANALYSIS

We arcsin transformed incubation constancy to improve normality of these data. We used correlational analyses to compare incubation constancy to daily weight loss, and incubation constancy to incubation period. We examined variation in daily incubation constancy in relation to day of incubation using ANCOVA with females as a factor and day of incubation as a covariate. We examined variation in daily recess frequency with females as a factor and day of incubation as a covariate. We examined variation in length of incubation recesses with females and hour as factors and ambient temperature and day of incubation as covariates. We examined variation in nest cooling during recesses with female as a factor and day of incubation, recess length, and ambient temperature as covariates. We included all first order interactions between factors and covariates in each of these ANCOVA analyses, but sequentially removed nonsignificant interactions from the final models based on type III mean square errors. All analyses were conducted using SAS (SAS Institute 1990), and means are presented \pm SE.

RESULTS

We measured weight change and incubation behavior of 19 females over 178 bird-days. Incubation constancy averaged $89.9 \pm 0.01\%$ and incubation period averaged 22.3 ± 0.5 days ($n = 19$). Average daily weight loss for incubating females was 16.5 ± 1.0 g day⁻¹ (range 8.3–26.8). From this, we estimated that females lost an average of 368 g during incubation, which represents 26% of the mass of females during early incubation. There was no relationship among females in daily weight loss and overall incubation constancy ($r = 0.02$, $P = 0.94$) or between overall incubation constancy and incubation period ($r = 0.13$, $P = 0.59$). The relationship between daily incubation constancy and day of incubation varied among females ($F_{18,140} = 3.0$, $P < 0.01$, Fig. 1).

Recess frequency averaged 2.4 ± 0.1 day⁻¹, but varied among females ($F_{18,143} = 3.57$, $P < 0.01$) and with day of incubation ($F_{1,143} = 4.02$, $P < 0.05$). Most recesses (70%) occurred between 10:00 and 22:00 (Fig. 2). Average recess length was 37.1 ± 0.9 min. The influence of incubation day on length of incubation recesses varied among females ($F_{18,418} = 2.52$, $P < 0.01$), and the influence of time of day on recess length varied with day of incubation ($F_{23,418} = 1.66$, $P =$

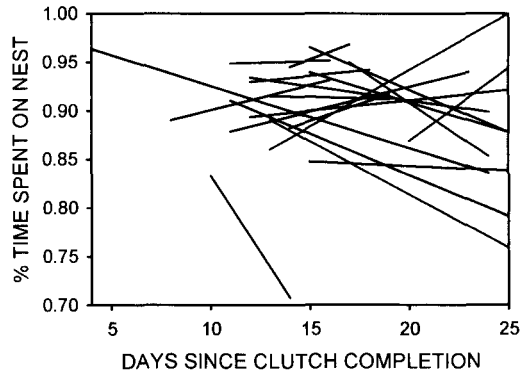


FIGURE 1. Relationships between daily incubation constancy and day of incubation for 19 Spectacled Eider females on the Yukon-Kuskokwim Delta, Alaska, in 1996. Each line represents the regression solution of daily incubation constancy for an individual female.

0.03). The length of incubation recesses did not vary with ambient temperature ($F_{1,418} = 0.66$, $P = 0.42$). Nests cooled an average of $4.2 \pm 0.1^\circ\text{C}$ during recesses. The amount of nest cooling experienced during recesses varied with ambient temperature ($F_{1,445} = 6.11$, $P = 0.01$). Additionally, the influence of length of incubation recess on cooling varied among females ($F_{18,445} = 2.65$, $P < 0.01$), and the influence of day of incubation on cooling varied among females ($F_{18,445} = 1.82$, $P = 0.02$).

DISCUSSION

Our measurement of incubation behavior using artificial eggs was restricted by methodological problems. The habit of eiders of defecating on their eggs when flushed from the nest (Swennen 1968, McDougall and Milne 1978) and high humidity in the nest microclimate caused the caps on the artificial eggs to stick. Additionally, data was lost due to failure of the data loggers, flooding of the data loggers, and failure of the switch and resistor in the artificial eggs. Thus, for many females, only a portion of the incubation period between captures was sampled (Fig. 1).

Afton and Paulus (1992) report a positive relationship between incubation constancy and weight loss among 33 species of waterfowl. The average incubation constancy we measured (90%) was lower than that reported for Common Eiders (96%) (Korschgen 1977). Accordingly, we estimated that female Spectacled Eiders lost 16.5 g day⁻¹ of incubation and in total lost 26% of their early incubation body weight compared to 23 g day⁻¹ and 33% total weight loss for Common Eiders (Korschgen 1977). Similar to our results, Kellett and Alisauskas (1997) report that King Eiders (*Somateria spectabilis*) lost 14.8 g day⁻¹ during late incubation and 24% of their body weight throughout incubation. The combination of these results support the assertion that there is a trade-off between incubation constancy and weight loss during incubation among species.

All females lost weight during incubation, but we found no indication that weight loss was related to

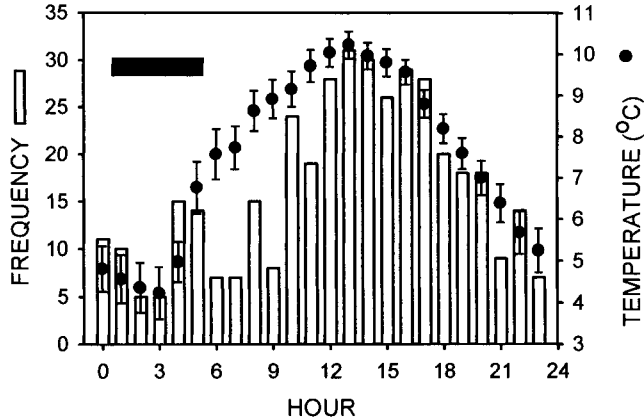


FIGURE 2. Frequency of incubation recesses (bars) and average ambient temperature (circles) by hour of day for 19 Spectacled Eider females on the Yukon-Kuskokwim Delta, Alaska. Hourly temperatures were averaged during the period that incubation behavior was monitored from 26 May 1996 through 21 June 1996; error bars represent the CV for the average temperatures. Shaded bar indicates average time from sunset to sunrise during the study.

incubation constancy among individual females. Contrary to the results of Aldrich and Raveling (1983) for Canada Geese (*Branta canadensis moffitti*), female Spectacled Eiders did not reduce weight loss during incubation by decreasing attentiveness. However, our study design did not allow us to examine variation in weight loss in relation to patterns of incubation constancy within females. Thus, we may lack detailed data required for a critical test of the relationship between incubation constancy and weight loss. Other studies have shown that patterns of weight loss are not constant throughout incubation (Aldrich and Raveling 1983). Additionally, the patterns of daily incubation constancy throughout incubation varied among females, and we only obtained information on incubation constancy for a portion of the incubation period (Fig. 1). However, even with daily measures of incubation constancy and weight, Mallory and Weatherhead (1993) failed to find a consistent positive relationship between incubation constancy and weight loss in Common Goldeneyes (*Bucephala clangula*). Alternatively, considerable among-female variation in daily weight loss during incubation has been reported for other species of waterfowl and may be related to variation in food abundance and availability (Gatti 1983, Harvey et al. 1989, Zicus and Riggs 1996). Little is known about the behavior of female Spectacled Eiders during incubation recesses, but they spend a portion of this time feeding (Dau 1974). Thus, some of the among-female variation in weight loss we observed may have been related to variation in foraging success.

The relationship between daily incubation constancy and day of incubation varied among females. Time spent on nests increased as incubation progressed for some females, but decreased for others (Fig. 1). Relative to day of incubation, studies of other waterfowl have documented general declines in incubation constancy (Aldrich and Raveling 1983, Mallory and Weatherhead 1993), or no change in daily incubation

constancy (Caldwell and Cornwell 1975, MacCluskie and Sedinger 1999); however, ours is the first study to demonstrate intraspecific (i.e., among female) variation in incubation constancy relative to day of incubation. Additionally, the relationship between recess length and day of incubation varied among females, whereas, the relationship between recess frequency and day of incubation was constant among females. Thus, it appears that variation in recess length was the primary cause of the among female variation in the relationship between day of incubation and daily incubation constancy.

Several studies have demonstrated a negative relationship between incubation constancy and egg development time (Aldrich and Raveling 1983, Wilson and Verbeek 1995, Zicus et al. 1995), whereas others have found no relationship (Eichholz and Sedinger 1998). We found no relationship between overall incubation constancy and incubation period for Spectacled Eiders. This suggests that incubation breaks, and associated egg cooling, were not costly in terms of egg development time for Spectacled Eiders. Thus, any costs associated with reduced nest attendance for Spectacled Eiders must be related to egg success in terms of hatchability and predation.

In many species of waterfowl, greater recess length has been associated with higher ambient temperatures (Afton and Paulus 1992). In this study, nest cooling was related to ambient temperature, yet females did not adapt the length of incubation recesses in relation to ambient temperatures. Similarly, no relationship between recess length and ambient temperature has been reported for Emperor Geese (*Chen canagula*), which also nest on the Yukon-Kuskokwim Delta, and Northern Shovelers (*Anas clypeata*) nesting in the subarctic (Thompson and Raveling 1987, MacCluskie and Sedinger 1999). However, Spectacled Eiders (Fig. 2) are similar to other species of waterfowl which have been shown to time recesses during the warmest portion of

the day (Thompson and Raveling 1987, Reed et al. 1995, MacCluskie and Sedinger 1999). Thus, Spectacled Eiders most frequently took incubation recesses mid-day when avian predators were active (Fig. 2), and egg loss due to avian predators on our study area was high (Flint and Grand 1996, Grand and Flint 1997). Therefore, our data do not support the hypothesis that the threat of predation influences the timing of incubation recesses (Hohman 1986, Swennen et al. 1993). We conclude that recesses were timed to take advantage of warmer ambient temperatures and that other factors influenced recess length (MacCluskie and Sedinger 1999).

Overall, we observed considerable individual (i.e., among female) variation in incubation behavior. Additionally, the patterns we observed relative to day of incubation for daily incubation constancy, recess length, and nest cooling varied among females. The combination of these results suggests considerable plasticity among females in incubation behavior (MacCluskie and Sedinger 1999).

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