INCUBATION BEHAVIOR OF NORTHERN SHOVELERS IN THE SUBARCTIC: A CONTRAST TO THE PRAIRIES[1]

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Abstract. We examined patterns of nest attendance of Northern Shovelers (*Anas clypeata*) at Minto Flats, Alaska to explore geographic variation in incubation rhythms between females nesting in Alaska and females nesting in the prairies of North America. Females nesting at Minto Flats exhibited lower incubation constancy than females from the mid-continent. Females nesting at Minto took 4.1 ± 0.1 recesses day^{-1}, twice as many as other *Anas* species nesting in the prairies, but length of recesses was not different than prairie nesting conspecifics. Timing of recesses was dissimilar to rhythms reported for Northern Shovelers in the prairies; many recesses were taken at midday, fewer recesses were taken in the morning and evening, and females were on nests less when ambient temperature increased. Variation in the number of recesses taken per day was explained by differences among females and day of incubation. Recess length varied both among females and with time of day the recess was taken. Our data suggest that females at Minto have more difficulty obtaining food resources during incubation than females in the prairies. Differences observed in attentiveness among females at Minto are likely related to variation in territory and female quality.

Key words: Anas clypeata, incubation, incubation constancy, nest attentiveness, Northern Shoveler.

Patterns of nest attendance during incubation have been described for several species of ducks, including Black Ducks (*Anas rubripes*; Ringelman et al. 1982), Common Goldeneyes (*Bucephala clangula*; Mallory and Weatherhead 1993, Zicus et al. 1995), Northern Shovelers (*Anas clypeata*; Afton 1980), and Wood Ducks (*Aix sponsa*; Wilson and Verbeek 1995). However, little is known about incubation rhythms of subarctic nesting ducks and how they compare to those of conspecifics nesting in the prairies. Northern Shovelers (hereafter Shovelers) are an abundant nesting species in interior Alaska (Petrula 1993) and provide a comparison to Shovelers in prairies (Afton 1980).

Shovelers in interior Alaska and the prairies initiate nests midway between earliest and latest nest initiating species (Afton 1980, Petrula 1993), clutch size is similar between the two areas (9.2 for interior Alaska vs. 10.0 for the prairies, Petrula 1993), and zooplankton

abundance, the primary food of Shovelers (Krapu and Reinecke 1992), is similar in the two areas (Jacobs 1992).

Ambient temperatures during the breeding season are similar between the two areas; although during May and June mean daily temperatures are warmer (17°C and 20°C, respectively) in interior Alaska than the prairies (11°C and 17°C, respectively, for prairie regions of Manitoba). Females in interior Alaska and the prairies differ as interior Alaska experiences 22 hr of daylight beginning 20 May (Selkregg 1974) compared to only 14 hr of daylight in Manitoba during the same period (van der Valk 1989).

We studied nest attendance of Northern Shovelers at Minto Flats to compare incubation rhythms of Northern Shovelers on a geographic scale; females nesting in the subarctic (Minto Flats, Alaska) vs. females nesting in the prairies of North America (Afton 1979). The second purpose of this study is to describe variation in incubation rhythms among females nesting in one location (Minto Flats, Alaska).

We hypothesized females nesting at Minto would exhibit similar patterns of nest attendance to females in Manitoba because rate of endogenous lipid reserve used during incubation is similar between females nesting in the two areas (MacCluskie 1997). Correspondingly, we predicted that Minto and prairie females would take the same number of recesses because taking more frequent recesses would be more energetically costly to females with regard to re-warming of clutches (Caldwell and Cornwell 1975). However, because daylight is continuous at Minto during the nesting season (civil twilight occurs during 3 hr of "sundown"), we predicted females at Minto would take recesses with equal frequency during all times of the day. Nest attendance to protect eggs from either freezing or overheating (Webb 1987) is unlikely to be necessary, and continuous daylight eliminates the advantage of females leaving nests at a particular time to avoid predators (Hohman 1986, Afton and Paulus 1992).

METHODS

We conducted this study during the summer of 1993 on Minto Flats, AK (64°50'N, 148°50'W). Petrula (1993) has described this area in detail. Shovelers nesting in this wetland complex used meadow habitat dominated by bluejoint grass (*Calamagrostis canadensis*), sedge (*Carex sp.*), and marsh five-finger (*Potentilla palustris*). Average date of nest initiation (i.e., the first day an egg is laid) by Shovelers was 30 May and the interval between initiation of the first and last nests (mean ± SD) was 40.0 ± 5.5 days (Petrula 1993). We initiated fieldwork on 15 May and conducted standard

searches for nests (Klett et al. 1986) from 08:00 to 14:00 each day. Nests were located when females were flushed from their nests. We individually numbered and candled eggs (Weller 1956) to determine the stage of incubation for each nest.

We placed an artificial egg in the center, bottom of each nest for monitoring both nest attendance and nest temperature. Artificial eggs were composed of auto-body filler and housed a thermistor probe, an in-line micro switch, and a 10,000-ohm resistor. The thermistor was connected to a single-channel data logger (OnSet Computer Corporation, Pocassett, Massachusetts) which recorded the temperature of the thermistor. For a more detailed description of the device, computer program, and equations for temperature transformation see Flint and MacCluskie (1995).

We recorded data every 4.8 min, which minimized the number of visits required to download data and still allowed adequate detection of changes in nest temperature. Nests were revisited every 6 days at which time the full data logger was removed and an empty data logger was connected to the thermistor. While we were at the nest site, artificial eggs were checked for proper operation and eggs were re-candled to check embryo development. After the initial nest visit, we timed revisits to nests when females were least likely to be present, which we determined from the first 6 days of nest attendance data. At some nests ($n = 6$) we could not put artificial eggs in during the initial visit, and we returned to those nests and put in artificial eggs after 14:00 to minimize disturbance to the female (Gloutney et al. 1993).

We also used thermistor probes and single-channel data loggers to record ambient temperature data at nests. Ambient temperature thermistor probes were affixed with plastic ties to a piece of vegetation at the height of the top edge of the nest bowl and adjacent to the nest. Ambient temperature data also were recorded at 4.8-min intervals, and data loggers were downloaded every 6 days. Data from ambient probes were used to determine an average hourly temperature, mean daily ambient temperature, and daily maximum and minimum temperatures.

Female absences < 14.4 min (3 sampling intervals) are likely a result of females repositioning themselves at nests and moving eggs, which Caldwell and Cornwell (1975) called "resettlements." This interval, therefore, provided a conservative estimate of time spent off the nest. Resettlements were not included in calculations of incubation rhythms.

We calculated incubation constancy for each female as the total percent of the incubation period spent on the nest. We determined daily attentiveness as the percent of each day a female was on the nest. When mechanical failure of switches occurred, attentiveness for that day was based upon the total number of hours during which the switch operated properly. Therefore, if a switch failed for 2 hr in one day, 22 hr was the maximum number of hours that a female could have been on the nest. We used data from days 3–22 of incubation in these calculations so that our methods were comparable to those of Afton (1980) and to facilitate comparisons of means. We tested for differences between means using two-tailed t-tests adjusted for the number of comparisons being made.

STATISTICAL ANALYSES

Previous studies (Zicus et al. 1995) suggest the repeated nature of nest attentiveness data poses statistical problems because a female's behavior on a particular day may be autocorrelated to her behavior the next day. Autocorrelation violates assumptions of linear statistical models (Neter et al. 1990), thus when linear models are used to evaluate such data, adjacent error terms tend to be of the same magnitude, and the variance of parameter estimates is underinflated. Therefore, we used the Durbin-Watson (D) test for autocorrelation to determine if this problem existed in our data (Neter et al. 1990). Values of D larger than the upper bound of the calculated test statistic indicate lack of autocorrelation in data. Subsequent data analyses were performed using females whose behavior was not autocorrelated.

We used ANCOVA (PROC GLM, SAS Institute 1992) models to test hypotheses about variation in percent of each day spent on nests, frequency of recesses, duration of recesses, and timing of recesses. In the most general models, we included all explanatory variables and all subsets of two-way interactions, and then eliminated interaction terms that did not explain a significant amount of variation in dependent variables. We used Type III Sums of Squares in evaluating the contribution of each variable to our models.

To model percent of each day a female spent on the nest, our initial model included female as a class variable, mean ambient temperature and day of incubation as covariates, and all two-way interactions. Length of recesses was modeled with ambient temperature and day of incubation as covariates, females and time of day the recess was initiated (time of day was divided into 4 classes of 6 hr each) as class variables, and all two-way interactions. Our model for variation in number of recesses taken per day included female as a class variable, while the covariates were ambient temperature, day of incubation, average length of recesses, and all two-way interactions.

To determine whether recesses were evenly distributed through the day, we first determined the proportion of recesses taken each day within each time of day category. In this model, proportion of recesses in a time of day category was the dependent variable, stage of incubation was included as a covariate, and time of day was nested in females to control for repeated observations of each female in each time-of-day category. To determine whether the proportions of recesses taken in each time-of-day category differed, we compared Least Square Mean estimates for each time of day controlled for stage of incubation and female. Values presented are means ± SE.

RESULTS

We monitored 14 female Shovelers for a total of 221 bird-days. However, for our analyses we used data only from 170 bird-days because we eliminated data from any day on which a nest was disturbed. For comparisons between females at Minto and Manitoba, we included data from all 14 birds we monitored. Mean incubation constancy of Shovelers nesting at Minto

TABLE 1.   Mean (± SE) incubation constancy, number of recesses per day, and recess duration for female Northern Shovelers nesting at Minto Flats, Alaska, Manitoba, Canada (Afton 1980), and all *Anas* sp. combined (Afton and Paulus 1992).

Parameter	Minto Flats, AK		Manitoba, Canada	All *Anas* sp.
Incubation constancy	72.8 ± 0.1	***a t_{24} = 45.4	84.6 ± 0.5	86 ± 1.4
Number of recesses day^{-1}	4.0 ± 0.1	*** t_{24} = 10.6	2.3 ± 0.1	2.2 ± 0.2
Recess duration (min)	86.9 ± 2.8	ns t_{24} = 1.5	93.8 ± 2.9	88 ± 10
n	14		12	11 species 16 studies

a Significance level of comparisons between adjacent columns: ns = nonsignificant, *** = $P \leq 0.001$.

was 18% lower than Shovelers nesting in Manitoba (Table 1). Consistent with lower incubation constancy, Minto females took almost twice as many recesses per day during incubation (range 2.0–5.2), however average length of recesses did not differ between females at Minto and Manitoba (Table 1).

Tests for autocorrelation of incubation behavior indicated that behavior was autocorrelated for 2 females, inconclusive for 2, and independent for 10. We report all further results excluding data from the autocorrelated and inconclusive females.

Female Shovelers at Minto varied in the proportion of each day they spent on nests ($F_{9,112}$ = 3.55, P < 0.001), and females tended to spend less time on nests as ambient temperature increased ($F_{1,112}$ = 3.51, P = 0.06) (Fig. 1). Day of incubation did not explain variation in the percent of day females spent on the nest ($F_{1,112}$ = 0.22, P = 0.64).

The number of recesses each day varied among females ($F_{9,118}$ = 2.20, P = 0.03), and by day of incubation ($F_{1,118}$ = 3.35, P = 0.07) (Fig. 2). The average length of recesses did not affect the number of recesses taken each day ($F_{1,118}$ = 1.55, P = 0.21), nor did ambient temperature ($F_{1,118}$ = 1.51, P = 0.22).

Females differed in the length of recesses they took each day ($F_{9,488}$ = 5.40, P < 0.001), and recess length varied with time of day the recesses were taken ($F_{3,488}$ = 8.15, P < 0.001) (Fig. 3). Neither day of incubation ($F_{1,488}$ = 0.20, P = 0.66) nor ambient temperature explained any variation in recess length ($F_{1,488}$ = 0.02, P = 0.89).

The percentage of recesses (16.8 ± 0.4% day^{-1}) taken was lowest and of shortest duration between 00:00 and 06:00 (61.4 ± 8.9 min) (Fig. 3). Between 07:00 and 12:00, 22.6 ± 0.2% day^{-1} of recesses were taken and averaged 72.0 ± 7.5 min. Most (35.0 ± 0.3%) recesses occurred from 13:00 to 18:00 and had the longest duration (99.2 ± 7.0 min). Between 19:00 to 23:50, 25.8 ± 0.2% day^{-1} of recesses were taken and averaged 82.7 ± 10.6 min.

DISCUSSION

Total incubation constancy and nest attendance patterns were different between Shovelers nesting at Minto and those nesting in the prairies of North America. Females nesting at Minto Flats were less attentive than females nesting in prairies. Correspondingly, the number of recesses taken each day by Shovelers at Minto
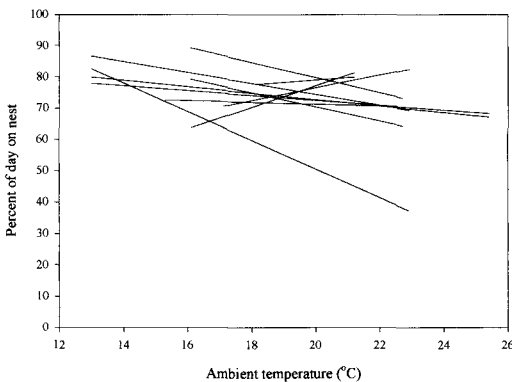

FIGURE 1.   Least square regression lines showing change in percent of day spent on nest as a function of ambient temperature for 10 Northern Shoveler females nesting at Minto Flats, Alaska.
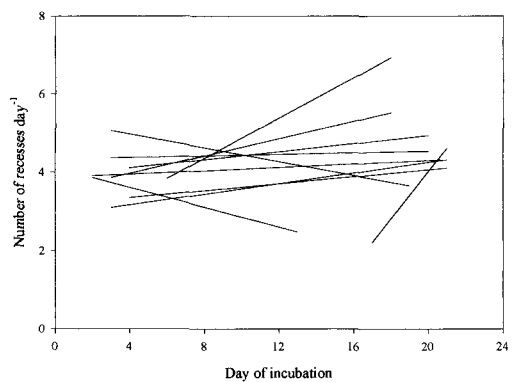

FIGURE 2.   Least square regression lines illustrating the number of recesses taken per day during incubation by 10 Northern Shoveler females nesting at Minto Flats, Alaska.
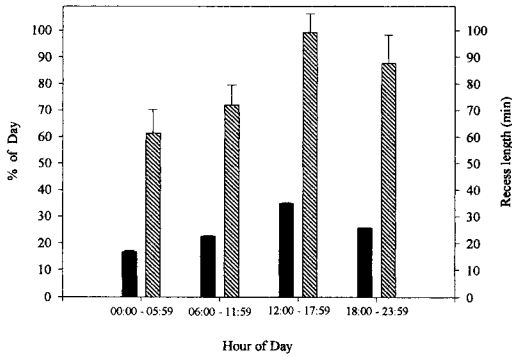
FIGURE 3. Distribution of mean (± SE) percentage of recesses (solid bars) taken during time-of-day categories and recess length during incubation (hatched bars) for 10 female Northern Shovelers nesting at Minto Flats, Alaska (n = 488 recesses).

was greater than the number taken by Shovelers in Manitoba, although the average length of recesses did not differ between Minto and Manitoba females. Our prediction that females nesting at Minto would exhibit similar incubation rhythms was not supported, and our data provide evidence of geographic variation in incubation rhythms within a species.

Females at Minto may be less attentive to their nests because of declining food abundance during incubation. Gizzard weight of incubating female Shovelers does not decrease through incubation (MacCluskie 1997), indicating females spend time feeding during incubation recesses because the gizzard serves as the primary site of food maceration in ducks (Duke 1986). Decline in gizzard weight is well documented in Anatids that feed little during incubation (Cantin et al. 1974). We do not have behavioral observations of females at Minto Flats during recesses, but Afton (1979) reported that female Shovelers on recesses spent the majority of their time feeding, and we assume that a similar pattern holds for Shovelers nesting at Minto.

Females nesting in Manitoba require endogenous nutrient reserves to produce eggs and to complete incubation (Ankney and Afton 1988). In contrast, females at Minto do not use body reserves to produce eggs (MacCluskie 1997), yet during incubation they deplete lipid reserves at a rate equivalent to females in Manitoba (MacCluskie 1997). This indicates that nutrients in food resources at Minto are adequate to meet nutritional demands during egg production, but food may be in short supply during incubation. The increase in number of recesses taken each day as incubation progresses supports this idea. Zicus and Riggs (1995) reported forage availability or quality could explain variation in weight loss patterns of Common Goldeneyes which exhibit incubation constancy similar to Shovelers. Our observations also suggest there may be seasonal differences between Minto and Manitoba in food availability relative to timing of nesting for this species.

Recess lengths were similar between females at Minto and Manitoba, however timing of recesses differed. Females in Manitoba took very few recesses between 10:00 and 13:00, the hottest portion of the day (Afton 1980), whereas females at Minto took many recesses during the same time interval (Fig. 3). During this study, daily maximum temperature and minimum averaged 28.2 ± 0.4°C and 11.3 ± 0.2°C, respectively, at nest bowls. Lethal effects of solar radiation may be rarely attained in interior Alaska, and females likely take advantage of warm temperatures when nests cool at slower rates to maximize recess length and/or frequency. Additionally, rates of nest cooling for Minto females are approximately half the value Afton (1980) reported for Shovelers nesting in Manitoba (MacCluskie 1997), facilitating a greater advantage of midday recesses.

Zooplankton migrate up the water column in response to diminishing light penetration through water (Cushing 1951). We suggest that observed daily incubation rhythms of females nesting at Minto represent a tradeoff between the advantage of taking recesses at midday when nests cool least and taking recesses at twilight when nests cool more rapidly but food is more available.

We consistently observed among-female variation in incubation rhythms (percent of day spent on nest, number of recesses day^{-1}, and length of recesses). Cooling rates of nests also varied among females nesting at Minto (MacCluskie 1997). Nest cooling rates are a function of nest microclimate (Afton and Paulus 1992) in addition to ambient temperature and thermal properties of the clutch. Not only is nest site selection important for successful hatching of eggs, it also is critical for Shovelers because territories include the female's feeding area and her nest (Seymour 1974). We suggest that observed among-female variation in incubation rhythms may be a result of individual optimization of reproductive effort in relation to such factors as body condition, nest-site microclimate, and food resources, which influence female behavior through reproduction. Hohman (1986), Zicus et al. (1995), and Flint and Grand (1999) are other studies which also provide evidence of among-female variation in incubation behavior in ducks. Our study expands this finding to the scale of geographic variation. Our results suggest that incubation behavior is a highly plastic characteristic which allows individuals to adapt their reproductive investment to specific local or geographic conditions (Flint and Grand 1999).

Given the among-female variation we observed between geographic areas and within the Minto sample, we suggest that to fully explain reproductive patterns observed in the wild (e.g., clutch size, incubation behavior), it is necessary to examine all portions of a reproductive attempt. Incubation is part of a reproductive cycle, not a discrete event. As such, female incubation behavior must be evaluated not only with respect to variables measured during incubation, but other variables such as body condition and food abundance (Afton and Paulus 1992, Ankney and Alisauskas 1992) should be taken into account in future studies.

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