

INCUBATION RHYTHMS AND MASS LOSS OF COMMON GOLDENEYES¹

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Abstract. We examined simultaneously incubation rhythms and mass loss of 16 female Common Goldeneyes (*Bucephala clangula*). On average, female goldeneyes spent 81% of the day incubating eggs, and took 2.7 recesses per day, each lasting an average of 114 min. Females began incubation approximately 20% heavier than the lowest body mass they reached over the incubation period, a slightly greater mass loss than predicted for ducks their size. Goldeneye incubation behaviors were similar to those reported for other Mergini, and were consistent with the general relationship between body size and incubation behavior in waterfowl. Females differed in how they varied their incubation behavior in response to incubation patterns on the previous day and environmental factors, although females typically responded to warmer temperatures by spending more time off the nest. Female goldeneyes appeared to manage their mass loss by modifying their incubation behavior. Females tended to lose less mass on days following more substantial mass loss, and once females approached their minimum mass they spent more time off the nest. However, not all females were successful in this approach. Two females may have deserted their nests because they had relatively high mass loss (>20%) and reached a low body mass (about 600 g), and thus could not maintain incubation sufficient to hatch their eggs without putting themselves at further risk.

Key words: *Incubation; incubation rhythm; mass loss; Common Goldeneye; Bucephala clangula.*

INTRODUCTION

Appropriate behavior by a bird during incubation is critical to reproductive success. On- and off-nest activities must be scheduled so that the thermal and gaseous requirements for development of the embryos are met (Drent 1973), while meeting the energetic requirements of the parent (e.g., Cartar and Montgomerie 1985, Drent et al. 1985). Increased investment in incubation by the parent to enhance embryonic development can only be achieved at a cost to the parent's physical condition or susceptibility to predation, thus reducing the parent's future reproductive success (Trivers 1972).

Nest attentiveness and the patterns of incubation (i.e., incubation rhythm) have been recorded for at least 35 species of waterfowl (reviewed in Afton and Paulus 1992). Because larger species are capable of storing greater nutrient reserves to sustain their metabolic requirements during incubation and use these reserves more efficiently, larger waterfowl species can spend a

greater proportion of their time incubating their clutch. Accordingly, larger waterfowl species lose proportionally more mass during incubation than smaller species. Females of most North American species attain their greatest annual body mass just prior to nest initiation, lose mass during egg-laying and incubation, and decline to their lowest annual mass at or shortly after hatching (reviewed in Alisauskas and Ankney 1992). If females lose too much mass during incubation, they may abandon clutches (e.g., Korschgen 1977), may die (e.g., Harris 1970, Korschgen 1977, Ankney and MacInnes 1978), or may not survive to breed the following year (Hepp et al. 1990). Despite these general patterns, there is considerable variation in individual responses of females to factors that can influence incubation rhythms and hence mass change (Ringelman et al. 1982, Hohman 1986, Aldrich and Raveling 1983).

Because of difficulty in obtaining continuous recordings of nest attentiveness and mass loss of incubating birds, few studies have examined these variables simultaneously. Thus, interpretation of incubation patterns and mass change necessarily have been based on correlation, drawing on results of separate studies. However, recent tech-

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nological advances enable researchers to monitor concurrently nest attentiveness and mass change under natural conditions (e.g., Jones 1987, Mulder and Swaan 1992), allowing direct comparison of incubation behavior and mass loss recorded during identical environmental conditions on individual birds.

We present here a comprehensive examination of incubation behavior and concurrent mass loss of the Common Goldeneye (*Bucephala clangula*). We simultaneously measured time spent on and off the nest as well as mass changes of female Common Goldeneyes using two types of remote, electronic monitoring systems (Mallory and Weatherhead 1992). There are few published records of goldeneye nest attentiveness or mass loss during incubation (see Afton and Paulus 1992), with the most complete information coming from work in Minnesota (Zicus unpubl., in Afton and Paulus 1992). Common Goldeneyes are medium-sized (approximately 700 g; Bellrose 1980), early-nesting, boreal ducks that rarely reneest (Zicus 1990). We examined whether incubation rhythms and mass loss of Common Goldeneyes conformed to the patterns observed in other North American waterfowl. We predicted that females would lose approximately 18.5% body mass during incubation, based on data for other North American waterfowl (Afton and Paulus 1992, p. 77). We also examined how individual females partitioned their time off the nest each day in relation to their behavior and mass change on the previous day, the stage of incubation, and concurrent and previous weather conditions. We predicted that females would spend more time on the nest when ambient temperatures were cooler or during rain (Afton and Paulus 1992), and that females that had lost more mass the previous day would spend more time off the nest.

METHODS

We studied Common Goldeneyes nesting in previously established nest boxes near Sudbury, Ontario in 1989 and 1990 (Mallory et al. 1993). All nest boxes were wooden, constructed to standard dimensions (22 × 25 × 47 cm), erected on large trees (≥25 cm diameters) at heights ≥3 m, had steel predator guards, faced the center of the lake (generally south-facing), and were "visible but isolated" (Semel et al. 1988). Thus, we assumed that effects on incubation behavior due to microhabitat differences were minimized.

Two incubation monitoring systems were used: a balance system ($n = 8$ females) and a load-cell system ($n = 8$ females) (Mallory and Weatherhead 1992). The balance system provided accurate measures (± 1 g) of mass recorded at approximately 6.5 min intervals. Periods of time spent on the nest were determined by multiplying the number of records of a consistent mass by the recording interval. The load-cell system provided continuous recording of nest attentiveness, and reliable but less accurate records (± 10 g) of mass than the balance system (Mallory and Weatherhead 1992). Both systems were installed just prior to or during the first week of incubation for 12 nests, while installation under four other clutches was delayed until the second week of incubation. The recording apparatus of both systems was located ≥ 10 m behind the nest box, so females usually did not flush when we checked the recording apparatus. Balance systems were checked every fourth day, while load cell systems were checked at least weekly.

We considered incubation to begin on the first night through which the female remained on the nest. We defined "incubation constancy" as the total time spent on the nest each day (expressed as a percent of 24 hr), and a "recess" as a period of time off the nest. For each continuous, one-day recording of behavior on the nest, we calculated incubation constancy, the number of trips off the nest ("recess frequency"), and the mean length of each trip ("recess duration"). The general patterns were then derived from the means of each of these variables calculated from the values for all females on each day of incubation. Incubation rhythm data from days on which females were caught were excluded from all analyses. We also recorded the maximum mass of each female for each recorded day of incubation. The lowest of these values (i.e., the lowest daily maximum) for each female was considered to be the minimum mass recorded during incubation. The result of dividing each daily maximum by the overall minimum recorded mass was then expressed as a percent of that minimum mass and termed "incubation mass." For example, if a female goldeneye weighed 660 g on the second day of incubation and the lowest recorded mass for that female during incubation was 600 g, then on day two her incubation mass was 110% (10% above her minimum recorded mass). We captured all but one of our monitored females once

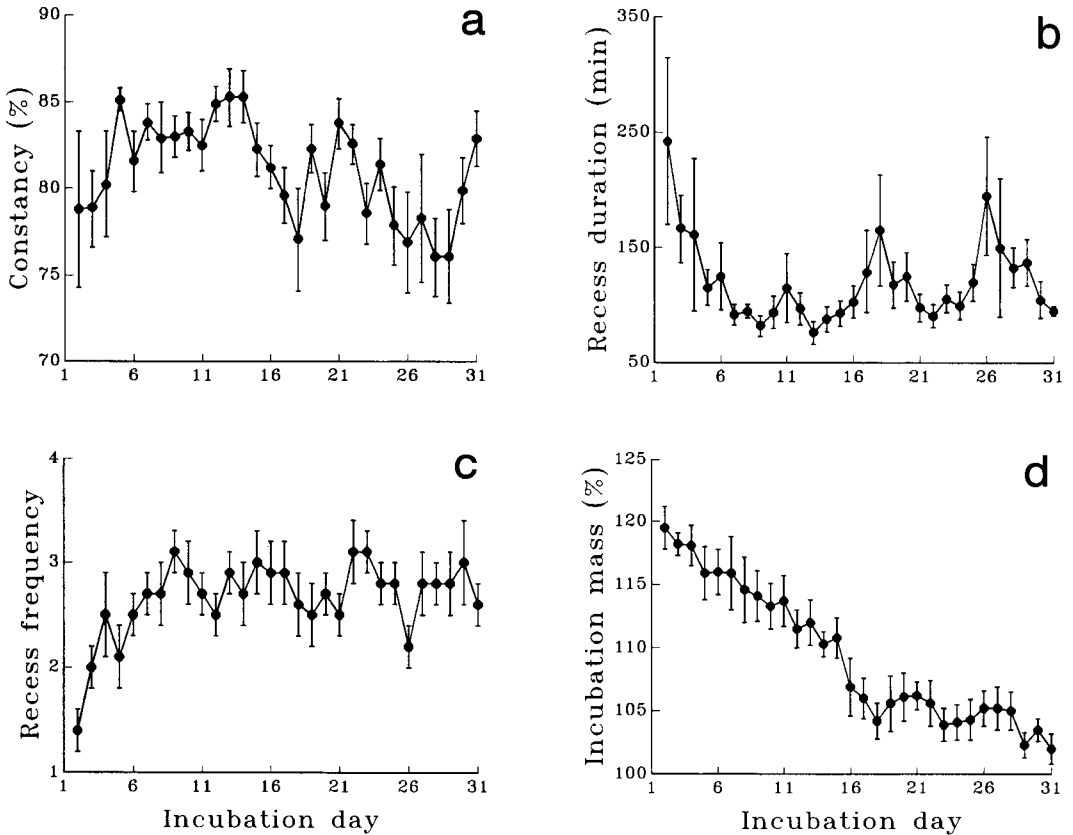


FIGURE 1. Relationships between incubation day and mean (a) incubation constancy, (b) recess duration (min), (c) recess frequency, and (d) incubation mass. For figures a, b, and c, circles (\pm SE) are mean values for a minimum of five and maximum of 13 females for each day of incubation. For figure d, circles (\pm SE) are mean values for a minimum of three and maximum of 10 females.

during incubation to corroborate their mass from the nest monitors by weighing them with a spring balance.

Ideally, the most accurate measure of minimum and maximum daily body mass would exclude the mass of ingesta and feces, but we could not control for effects of consumption or defecation when measuring body mass by remote monitoring systems. Therefore we had to rely on our measures of maximum daily mass, recognizing that some variation in body mass would be due to ingesta. This variation should not be biased in any systematic way for the patterns we examined.

Weather data (mean daily air temperature [$^{\circ}$ C], total precipitation [mm], and average wind speed [km/hr]) were obtained from Environment Canada records at the Sudbury airport, located within 50 km of all nests.

All statistical analyses were performed using the SAS Inst. (1988) software package. General patterns of incubation behavior and mass loss were examined on pooled data using linear regression. Individual patterns of incubation behavior and mass loss were examined using Spearman rank correlations and stepwise multiple regression (see results). All means are reported \pm SE.

RESULTS

GENERAL PATTERNS OF NEST ATTENTIVENESS

Female goldeneyes incubated clutches for about 31 days at our study site, but some completed incubation in 30 days. Females did not establish a consistent rhythm until day five, and vocalizations from the embryos may have affected fe-

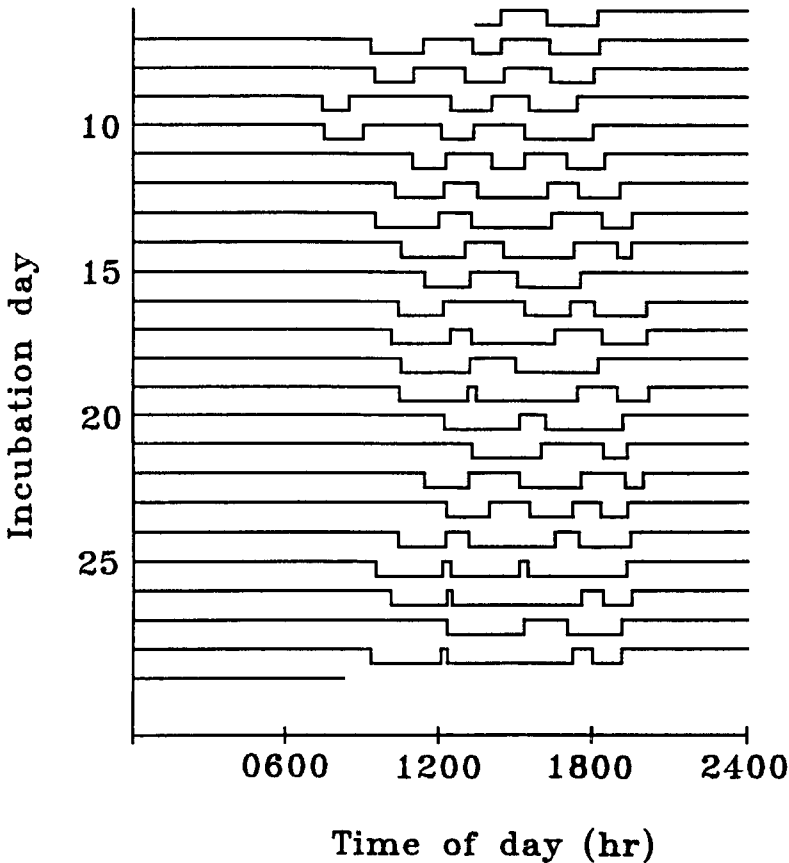


FIGURE 2. The incubation pattern of a female Common Goldeneye (Lake 922) monitored from day six to day 29 of incubation. Each horizontal line represents a 24 hr day, and depressions in a line represent periods off the nest.

male behavior after day 29 (Fig. 1). For these reasons, we restricted our analyses on incubation rhythm to the period from day five to day 29. Sixteen female Common Goldeneyes spent $81.2 \pm 0.4\%$ of the day incubating (range 57.0–95.1%), and took 2.7 ± 0.1 recesses per day, for an average duration of 114 ± 5 min. However, patterns of incubation were not static (Fig. 1). As incubation proceeded, female goldeneyes spent less time on the nest ($r = -0.75$, $df = 24$, $P < 0.001$; Fig. 1a), particularly after the midpoint of the incubation period. Incubation constancy was higher when females took shorter recesses ($r = -0.77$, $df = 24$, $P < 0.001$), but constancy was not correlated significantly with recess frequency ($r = -0.08$, $df = 24$, $P = 0.6$). Females took longer recesses later in incubation ($r = 0.49$, $df = 24$, $P = 0.01$; Fig. 1b), while recess frequency remained constant ($r = 0.17$, $df = 24$, $P = 0.42$;

Fig. 1c). When female goldeneyes took long recesses, they took fewer recesses per day ($r = -0.47$, $df = 24$, $P = 0.02$).

Figure 2 depicts the incubation pattern of a female goldeneye, recorded from day six to day 29. Only one nocturnal recess was recorded for any female, for a duration of approximately 5 min. For four females that began incubation within six days of each other (thereby subjected to similar ambient temperatures during incubation), we recorded the times when females left the nest (Fig. 3). Females took their first recess by 12:00, and returned from their last recess by 20:00.

GENERAL PATTERNS OF MASS LOSS

Female masses recorded by the monitoring systems were within 9.5 ± 2.9 g ($n = 11$) of masses taken on the same day with spring balances. This

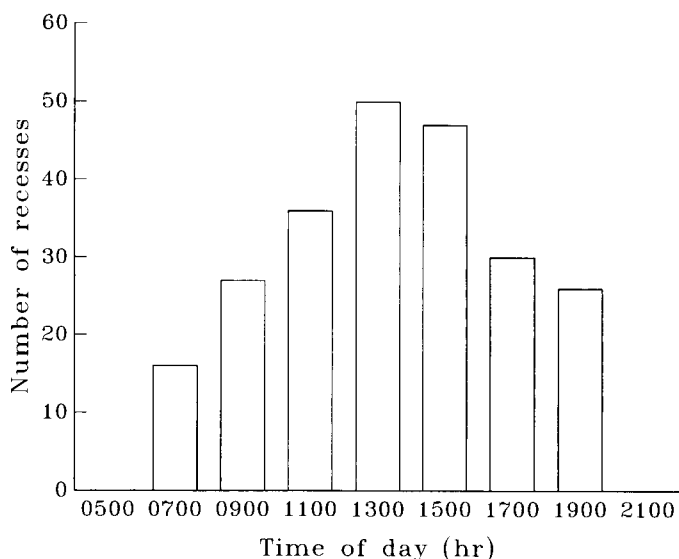


FIGURE 3. The distribution of incubation recesses in relation to the time of day, recorded for four female Common Goldeneyes that initiated nests within six days of each other.

mean difference is well within the daily variation in body mass recorded for females (Mallory, unpubl. data), so we are confident that masses recorded by the systems were reliable. Female goldeneyes lost mass during incubation ($r = -0.75$, $P < 0.01$; Fig. 1d). However, the rate of mass loss in goldeneyes decreased later in incubation, and is best described by the equation:

$$I = 0.01(D)^2 - 1.1(D) + 121.7,$$

where I is incubation mass and D is the day of incubation, including data from day one to day 31 ($r^2 = 0.61$, $F = 157$, $df = 2, 201$, $P < 0.001$). Female goldeneyes began incubation approximately 20% heavier than the lowest mass they attained during incubation. The mean mass change from the start to end of incubation was a loss of $16.7 \pm 0.6\%$ ($n = 10$ females). Minimum masses were attained as early as day 18 for some females, but typically occurred after day 21.

WEATHER DURING INCUBATION

Weather near Sudbury during the nesting season of 1989 and 1990 was similar to the average weather over the last two decades, although 1990 had more precipitation than usual (from Environment Canada weather records). Mean daily weather conditions during each breeding season were as follows: 1989; mean temperature, 15.0°C ; total precipitation, 3.3 mm; average wind speed,

12.1 km/hr; 1990; mean temperature, 13.0°C ; total precipitation, 4.1 mm; average wind speed, 14.2 km/hr. Warmer days tended to be less windy in both years (Spearman rank correlations, $P < 0.05$), and days with rain were cooler in 1989 (Spearman rank correlation, $P < 0.05$). Because each of these variables can have a distinct effect on incubation scheduling (Cartar and Montgomerie 1985, 1987), we consider them separately below.

INDIVIDUAL VARIATION IN INCUBATION AND MASS LOSS

In addition to the overall patterns of incubation for Common Goldeneyes, we also examined how individual females partitioned their time off the nest each day in relation to their behavior on the previous day (also referred to hereafter as previous behavior), the stage of incubation, and concurrent and previous weather. Therefore, we calculated correlations between weather or previous behavior and each female's daily incubation constancy, mean recess duration and recess frequency (Cartar and Montgomerie 1987). We used data collected between day five and 29 on the six females (one monitored in 1989 and the rest in 1990) for which we had the most complete data. These females were analyzed separately because there were significant differences between females in each of the three incubation rhythm

TABLE 1. Mean nesting and incubation characteristics of six female goldeneyes monitored between day five and day 29 of incubation. Numbers in parentheses are standard errors. Female mass is the mass on the day of capture and banding (usually week three of incubation).

| Variable | Female | | | | | |
|-------------------------------|--------------|------------|--------------|------------|------------|-------------|
| | 16 | 199 | 316 | 524 | 921 | 922 |
| Nest initiation date | May 23 | May 6 | April 30 | May 1 | May 17 | May 25 |
| Clutch size | 6 | 9 | 8 | 8 | 10 | 7 |
| Female mass (g) | >720 | 710 | 681 | 693 | 659 | 689 |
| Mean incubation constancy (%) | 79.4 (6.6) | 82.3 (6.2) | 81.2 (5.7) | 83.9 (4.0) | 81.9 (4.8) | 75.3 (4.3) |
| Mean recess duration (min) | 174.4 (23.9) | 82.1 (8.5) | 126.1 (28.7) | 80.6 (5.1) | 96.1 (4.4) | 129.9 (7.3) |
| Mean recess frequency | 1.8 (0.1) | 3.0 (0.1) | 2.7 (0.2) | 3.0 (0.1) | 2.7 (0.1) | 2.8 (0.1) |
| Sample size (days) | 20 | 23 | 19 | 25 | 23 | 22 |

components (One-way analysis of variance, all $P_s < 0.05$). To determine which of the independent variables best predicted constancy or recess duration, we used stepwise multiple regressions (maximum R^2 criterion; SAS Inst. 1988). These regression equations were used only to imply which independent variables influenced most strongly each bird's incubation scheduling. We could not use regression analysis to examine recess frequency because data were not continuous nor normally distributed.

To examine whether mass change of individual females was related to incubation rhythms or weather, we calculated daily mass change of four females. The mass change for a female on a given day was the difference between the maximum recorded mass and the minimum recorded

mass over the 24 hr period. Spearman rank correlations were used to compare each female's daily mass loss to her behavior in the previous day, her concurrent behavior, and weather variables.

Individual females differed considerably in their mean incubation rhythm characteristics (One-way ANOVAS, all $P_s < 0.05$; Table 1), and in their responses to factors that could influence incubation scheduling (Tables 2–4). For example, female 316, the earliest-nesting female we monitored, showed no predictable pattern in the amount of time spent off the nest each day in relation to any of the measured variables (Table 2), and had the highest variation in mean recess duration (Table 1). In contrast, the amount of time that the latest-nesting goldeneye, female

TABLE 2. Relationships between daily incubation constancy and the following variables: constancy the previous day, incubation stage, concurrent weather and weather the previous day (Spearman rank correlations, * = $P < 0.10$; ** = $P < 0.05$; *** = $P < 0.01$). Stepwise multiple regressions were used only to infer which variables had the greatest influence on each female's constancy (maximum R^2 criterion; numbers in parentheses represent variables that entered significantly in the regression for that female at $P < 0.05$).

| Variable | Female | | | | | |
|--|----------|-----------|-------|----------|-----------|-----------|
| | 16 | 199 | 316 | 524 | 921 | 922 |
| Constancy in previous day | 0.19 | 0.57*** | 0.25 | 0.56*** | 0.20 | 0.41* |
| Incubation day | (0.44*) | (0.69***) | -0.06 | 0.44** | 0.18 | 0.45** |
| Concurrent weather factors | | | | | | |
| Temperature | (0.48**) | 0.50** | -0.14 | (0.24) | (0.61***) | (0.80***) |
| Precipitation | -0.37 | 0.44** | 0.16 | 0.30 | -0.21 | -0.41* |
| Wind | -0.32 | 0.24 | 0.06 | (0.46**) | -0.28 | -0.18 |
| Previous day's weather | | | | | | |
| Temperature | 0.20 | 0.22 | -0.34 | 0.26 | 0.27 | 0.60*** |
| Precipitation | -0.16 | 0.14 | 0.12 | (0.11) | 0.28 | -0.23 |
| Wind | 0.26 | 0.27 | 0.18 | 0.26 | -0.14 | -0.39* |
| Variation explained by multiple regression | 53% | 35% | ns | 55% | 62% | 73% |
| Sample size (days) | 20 | 23 | 19 | 25 | 23 | 22 |

TABLE 3. Relationships between mean recess duration and the following variables: mean recess duration the previous day, incubation stage, concurrent weather and weather the previous day (Spearman rank correlations, * = $P < 0.10$; ** = $P < 0.05$; *** = $P < 0.01$). Stepwise multiple regressions were used only to infer which variables had the greatest influence on each female's mean recess duration (maximum R^2 criterion; numbers in parentheses represent variables that entered significantly in the regression for that female at $P < 0.05$).

| Variable | Female | | | | | |
|--|--------|-----------|------------|----------|-------|-----------|
| | 16 | 199 | 316 | 524 | 921 | 922 |
| Mean recess duration in previous day | 0.08 | 0.43** | 0.46** | 0.44** | 0.06 | 0.62*** |
| Incubation day | 0.31 | 0.51*** | -0.51** | 0.49** | 0.09 | (0.55***) |
| Concurrent weather factors | | | | | | |
| Temperature | 0.50** | (0.54***) | -0.29 | (0.40**) | 0.09 | (0.78***) |
| Precipitation | -0.01 | 0.21 | -0.04 | 0.39* | -0.32 | -0.53** |
| Wind | -0.24 | 0.03 | -0.06 | 0.26 | -0.30 | (-0.01) |
| Previous day's weather | | | | | | |
| Temperature | 0.32 | 0.32* | (-0.62***) | 0.44** | -0.09 | (0.85***) |
| Precipitation | 0.04 | 0.13 | (-0.20) | 0.26 | -0.12 | -0.25 |
| Wind | 0.19 | 0.26 | 0.09 | 0.13 | -0.03 | -0.29 |
| Variation explained by multiple regression | ns | 37% | 93% | 61% | ns | 90% |
| Sample size (days) | 20 | 23 | 19 | 25 | 23 | 22 |

922, spent off the nest daily was significantly correlated to more than half of the factors (Table 2), and this female had relatively low variation in mean recess duration (Table 1). Despite these differences between individuals, some consistent patterns of incubation rhythms among females were found.

Consistent with the general incubation patterns described above, four of six females spent more time off the nest each day as incubation proceeded (Table 2), which was achieved by tak-

ing longer recesses later in incubation (Table 3) without varying the frequency of recesses (Table 4). The behavior of a female on the previous day was positively correlated with her behavior the next day (Tables 2, 3). For both concurrent and previous day's weather variables, only temperature was a consistently useful predictor of incubation scheduling; females spent more time off the nest for longer trips when temperatures were warmer (Tables 3, 4). In fact, mean daily temperature (either concurrent or previous day's) was

TABLE 4. Relationships between recess frequency and the following variables: recess frequency the previous day, incubation stage, concurrent weather and weather the previous day (Spearman rank correlations; * = $P < 0.10$; ** = $P < 0.05$; *** = $P < 0.01$).

| Variable | Female | | | | | |
|------------------------------------|---------|-------|--------|---------|---------|---------|
| | 16 | 199 | 316 | 524 | 921 | 922 |
| Number of recesses in previous day | -0.29 | -0.01 | 0.59** | -0.02 | 0.31 | -0.05 |
| Incubation day | 0.05 | -0.28 | 0.54** | -0.29 | 0.02 | -0.23 |
| Concurrent weather factors | | | | | | |
| Temperature | 0.07 | -0.35 | 0.45* | -0.37* | 0.54*** | -0.04 |
| Precipitation | -0.40* | 0.14 | 0.11 | -0.31 | -0.08 | 0.29 |
| Wind | -0.23 | -0.05 | -0.20 | 0.24 | -0.09 | -0.27 |
| Previous day's weather | | | | | | |
| Temperature | -0.05 | 0.40* | 0.47** | -0.43** | 0.25 | -0.50** |
| Precipitation | -0.52** | -0.11 | -0.20 | -0.20 | 0.14 | 0.12 |
| Wind | -0.03 | -0.12 | -0.37 | 0.14 | -0.17 | -0.11 |
| Sample size (days) | 20 | 23 | 19 | 25 | 23 | 22 |

TABLE 5. Relationships between daily mass change and the following variables: day of incubation, concurrent incubation behavior and weather, and incubation behavior and weather the previous day (Spearman rank correlations, * = $P < 0.10$; ** = $P < 0.05$; *** = $P < 0.01$).

| Variable | Female | | | |
|-----------------------------|--------|-------|----------|-------|
| | 16 | 199 | 316 | 921 |
| Mass change in previous day | -0.21 | -0.26 | -0.02 | -0.37 |
| Incubation day | 0.13 | 0.12 | 0.13 | 0.02 |
| Concurrent conditions | | | | |
| Incubation constancy | -0.22 | 0.25 | -0.50* | 0.06 |
| Recess duration | -0.35 | 0.16 | -0.22 | -0.14 |
| Recess frequency | 0.26 | 0.14 | 0.17 | 0.18 |
| Temperature | 0.03 | 0.10 | 0.30 | -0.12 |
| Precipitation | 0.06 | -0.05 | -0.16 | -0.01 |
| Wind | -0.17 | -0.08 | -0.39 | 0.30 |
| Previous day's conditions | | | | |
| Incubation constancy | 0.46** | -0.17 | -0.25 | -0.22 |
| Recess duration | 0.22 | -0.18 | -0.15 | 0.14 |
| Recess frequency | 0.16 | 0.06 | 0.10 | -0.34 |
| Temperature | 0.12 | -0.32 | 0.17 | -0.15 |
| Precipitation | -0.10 | -0.08 | -0.76*** | -0.13 |
| Wind | -0.12 | -0.01 | -0.63*** | -0.09 |
| Sample size (days) | 19 | 24 | 13 | 21 |

the dominant variable identified in stepwise multiple regressions as influencing incubation constancy and mean recess duration. Given this pattern within females, we used the pooled data from all 16 females monitored between day five and 29 (see above) and tested whether a general relationship existed between incubation constancy and temperature. Indeed, for 254 days of records, females spent more time off the nest on warmer days ($r_s = 0.44$, $P < 0.001$).

Daily mass change was significantly correlated with incubation behavior for only one female (Table 5). For female 16, increased time spent incubating the eggs the previous day corresponded to decreased body mass the following day. For female 316, there was also a trend for body mass to decrease on days when the female spent more time on the nest. For all females, daily mass change tended to be opposite to the change in the previous day, that is, large losses were usually followed by a day of maintenance or even slight gain in mass (Table 5). Collectively, however, daily changes in body mass were not well-correlated to incubation behavior. Similarly, daily mass change was not significantly correlated to weather conditions for most females (Table 5). However, correlations between daily precipitation or wind speed and female mass change were consistently negative (significant for female 316),

suggesting that females tend to lose slightly more mass in poor weather.

CONSEQUENCES OF MASS LOSS DURING INCUBATION

Two of 16 monitored females deserted their nests before the end of their incubation period. We suspect that the pattern of mass loss for these females may have caused them to desert. The mean difference between measured mass at the start and end of incubation for eight successful and two unsuccessful females was $17.8 \pm 1.3\%$, and the mean mass of these females at the end of incubation was 626 ± 13 g. However, the two females that deserted began incubation 23.0 and 20.3% heavier than when they deserted (day 18 and 24 respectively), at which time they weighed 605 and 600 g respectively. Only two other females completed incubation at lower masses (579 and 574 g), but these females did not lose as much mass during incubation (12.0 and 15.2% respectively), and thus may have remained in better physical condition at the end of incubation than the females that deserted.

DISCUSSION

After attaining a consistent incubation rhythm, female Common Goldeneyes spent more time off the nest and lost mass as incubation pro-

ceeded. These patterns are consistent with those of other temperate-nesting waterfowl (reviewed in Afton and Paulus 1992). For most waterfowl species that have been studied, incubating females establish a pattern of daily nest attendance (Afton and Paulus 1992). Furthermore, a general relationship exists within and among waterfowl tribes in that larger species tend to have higher incubation constancy (Afton and Paulus 1992). Our measure of mean incubation constancy in Common Goldeneyes (81%) is in the same range as values reported previously (75%, Siren 1952; 85–89%, Semenov-Tyan-Shanskii and Bragin 1969; 82%, Zicus unpubl. in Afton and Paulus 1992), and are similar to values for other ducks of similar mass and to values for the Tribe Mergini (Afton and Paulus 1992). Therefore, our findings agree with the general relationship between body size and incubation constancy among waterfowl (Afton and Paulus 1992).

Female goldeneyes spent less time incubating the clutch as incubation proceeded, achieved in part by taking longer recesses each trip off the nest. Similar incubation behavior has been observed in White-winged Scooters, *Melanitta fusca deglandi* (Brown and Fredrickson 1987), Cinnamon Teal, *Anas cyanoptera* (Hohman 1991), and Northern Shovelers, *A. clypeata* (Afton 1980), although there are exceptions (e.g., Ring-necked Ducks, *Aythya collaris*, Hohman 1986). Female goldeneyes may be able to spend more time off the nest later in incubation because ambient temperatures are higher. In support of this hypothesis, goldeneyes initiating nests later in the breeding season had lower incubation constancy (Table 1). Also, mean daily temperature was the main factor that influenced incubation rhythms of six closely monitored females. Another factor that may allow female goldeneyes to spend more time off the nest as incubation proceeds is that developing embryos generate more heat later in incubation (Drent 1970). Both higher ambient temperatures and increased embryonic heat production would contribute to slower egg-cooling rates later in incubation (Drent 1970, Caldwell and Cornwell 1975).

Afton (1980) observed that Northern Shovelers rarely left the nest between 10:00 hr and 13:00 hr, and proposed that female shovelers remained on the nest during this period to protect the eggs from overheating. Two other ground-nesting species, Cinnamon Teal and Blue-winged Teal (*Anas discors*), exhibit similar nest atten-

tiveness (Glover 1956, Hohman 1991). Because direct sunlight does not affect eggs sheltered in a cavity, we expected that goldeneyes would not be constrained by this factor, and therefore would take recesses near midday. Common Goldeneyes often were off the nest at midday (Fig. 3), as was another cavity-nester, the Bufflehead (*Bucephala albeola*) (Erskine 1972). While data from these five species support the hypothesis that ambient temperature affects incubation rhythms of open- and cavity-nesting species differently, there are exceptions to this pattern. Hohman (1986) found that Ring-necked Ducks, an open-nesting species, often were off the nest at midday, while both Breckenridge (1956) and Stewart (1962) found that Wood Ducks (*Aix sponsa*), a cavity-nesting species, were on the nest at midday. Collectively, these results suggest that, in addition to exposure to direct sunlight, other characteristics of nest sites or nesting habits influence recess scheduling between species.

An additional factor that might affect incubation rhythms is previous breeding experience. Female Canada Geese (*Branta canadensis*) with previous breeding experience exhibit higher nest attentiveness than inexperienced breeders (Aldrich and Raveling 1983). In our study, female 316 was the only one of the six females that we knew had previous breeding experience (based on returning marked birds and high nest site fidelity; Mallory, unpubl. data). This female adjusted recess frequency and recess duration according to ambient weather (Tables 3, 4) to maintain relatively similar incubation constancy under all conditions (Table 2), while the inexperienced females spent significantly more time off the nest on warmer days. However, this female did not have higher incubation constancy than the others.

Incubation rhythms of Common Goldeneyes also were influenced by behavior or weather on the previous day. These results are consistent with earlier studies that suggest that previous conditions can influence incubation (Webb and King 1983), possibly by affecting levels of endogenous reserves (hence body mass; Cartar and Montgomerie 1987). By measuring body mass and nest attentiveness simultaneously, we were able to test this hypothesis directly, but our data do not provide clear support for it. Four females monitored for daily mass change tended to oscillate in daily mass, maintaining or gaining mass one day, then losing mass the following day.

However, daily mass change corresponded to previous behavior for only one female. Undoubtedly the availability of exogenous food resources (Hohman 1986b) and foraging success during recesses would influence the relationship between mass change and incubation rhythms, and mass change itself.

Common Goldeneyes at our site lost approximately 20% body mass during incubation, in agreement with the prediction based on mass loss in other North American ducks (Afton and Paulus 1992, p. 77). The pattern of mass loss in goldeneyes is similar to another member of the Tribe Mergini, the White-winged Scoter (Kehoe 1989). The heavier scoter loses slightly more mass during incubation (22%; Kehoe 1989), but both species reach minimum incubation mass around day 20. This stage of incubation may represent the time period when females of this tribe have used up remaining endogenous reserves and must switch to relying primarily on exogenous nutrient sources to meet the metabolic requirements of incubation (Brown and Fredrickson 1987, Afton and Paulus 1992). In support of this contention, goldeneyes spent noticeably more time off the nest after the midpoint of incubation (Fig. 2a). During incubation recesses, Common Goldeneyes (Mallory, unpubl. data), White-winged Scoters (Brown and Fredrickson 1987) and most other female waterfowl (Afton and Paulus 1992) spend most of their time feeding.

Gloutney and Clark (1991) stressed the importance of female body mass on incubation success in Mallards (*Anas platyrhynchos*) and shovellers, and suggested that differences in body mass could explain much of the intraspecific variation in incubation behavior. Hepp et al. (1990) also showed that the body mass of female Wood Ducks at the end of incubation was correlated with female survival, suggesting that incubation behavior is an important cost of reproduction. These three species are all capable of reneesting, and the mass of females influences their ability to initiate a second or replacement clutch (e.g., Kennamer and Hepp 1987). Because goldeneyes are unlikely to renest (Bellrose 1980, Zicus 1990) and thus may invest relatively heavily in their clutch, differences in mass loss during incubation may strongly affect annual and lifetime reproductive success, as is found in Common Eiders (*Somateria mollissima*) (Korschgen 1977). Our data are consistent with this hypothesis, because the female goldeneyes that deserted their nests had

relatively high mass loss and low body masses, suggesting they may have reached critically low body condition. However, a study of longer duration is required to determine the relationship between incubation rhythm, mass loss and survival of female Common Goldeneyes.

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