

# Incubation Behaviour of Greater Scaup *Aythya marila* on the Yukon-Kuskokwim Delta, Alaska

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This study examined the incubation behaviour of Greater Scaup *Aythya marila* on the Yukon-Kuskokwim Delta, Alaska. The goals of the study were to describe the incubation behaviour of Greater Scaup in terms of incubation constancy, recess frequency and recess length. The use of endogenous reserves by Greater Scaup was examined by determining weight loss over the incubation period. Further, intraspecific variation in incubation constancy was considered in terms of hypotheses regarding timing of reproduction. Constancy (% time on nest) averaged 59% during egg laying and increased to 83% during incubation. Patterns of daily incubation constancy varied among females, with no overall trend. Females took an average of 4.3 recesses per day, with an average length of 57 minutes. Body mass declined by 6.4 g day<sup>-1</sup> and females initiating nests later tended to be lighter. These data suggest that while Greater Scaup utilise some stored reserves during incubation, they probably meet most of their energetic demands by foraging during incubation recesses. These data are not consistent with the hypothesis that females are initiating nests before adequate forage is available in the spring to meet the demands of egg production and maintenance. Thus, the observed delay in the onset of nesting by Greater Scaup, relative to other sympatric nesting species, does not appear to be related to inadequate forage to meet nutritional requirements.

**Key Words:** incubation behaviour, incubation constancy, nest attentiveness, exogenous resources, body condition, weight loss

In many cases, waterfowl breeding at high latitudes rely on stored reserves to produce eggs. However, available reserves must be partitioned between investment in eggs and retention for use during incubation as female waterfowl typically rely on stored reserves to meet a portion of their maintenance requirements during incubation (Afton & Paulus 1992; Erikstad *et al.* 1993). Given that reserves are used during incubation and assuming that some forage is available to females, it has been suggested that females can modify their weight loss by adjusting their incubation constancy (Mallory & Weatherhead 1993). In support of this hypothesis, Afton & Paulus (1992) report a positive relationship between incubation constancy and weight loss among waterfowl species. Selection pressures influencing timing of reproduction probably influence this trade-off. That is, in order to optimise reproductive output, some waterfowl (eg arctic-nesting geese) may begin breeding before forage is available to incubating females (Raveling 1979; Sedinger & Raveling 1986). Accordingly, there may be a negative relationship between timing of nest initiation and the quantity of reserves required to support females during incubation. Early-nesting females must, therefore, rely on stored reserves, whereas later-nesting females can utilise available exogenous resources to a greater extent. Raveling (1979) noted that available forage for geese became progressively more abundant during incubation. In this sit-

uation, nest attendance patterns would probably change as incubation progresses. Early in incubation, nest attendance and associated mass loss should be high as there is little benefit in attempting to forage. Conversely, later in incubation, when forage is more abundant, females might reduce further mass loss by reducing nest attendance and spending more time foraging (Afton & Ankney 1991).

Reducing nest attendance is a strategy that might allow females to maintain body condition during incubation. However, there is likely to be a cost associated with reduced nest attendance. High incubation constancy allows females to maintain favourable environmental conditions within the nest, which enhances egg-hatchability (Afton & Paulus 1992). Additionally, females that are more attentive to the nest may have shorter incubation periods (Aldrich & Raveling 1983; Wilson & 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 minimise exposure to predation (Afton 1980; Hohman 1986; Swennen *et al.* 1993). Given that gulls appear to be an important predator in this study area (P.L. Flint, unpublished data), egg loss may be a significant cost of low nest attendance. The combination of these costs to incubating females has led to the

suggestion that incubation behaviour is a trade-off between loss of body condition, maintenance of egg viability and risk of predation (Thompson & Raveling 1987; Afton & Paulus 1992).

Greater Scaup *Aythya marila* nest relatively late, compared to other waterfowl, on the Yukon-Kuskokwim Delta, Alaska (P.L. Flint, unpublished data). Further, they lay large clutches of large eggs (Flint & Grand 1999a). Total clutch volumes of Greater Scaup exceed those of Black Brant *Branta bernicla nigricans* and approach volumes of Lesser Snow Geese *Anser caerulescens caerulescens* (Ankney & Bisset 1976; Flint & Sedinger 1992; Flint & Grand 1999a). The combination of late nesting and high investment in clutches leads to the hypothesis that Greater Scaup rely heavily on exogenous resources for the production of eggs. Accordingly, a similar use of exogenous resources during incubation was predicted. Specifically, this prediction implies that Greater Scaup will have relatively low nest attendance and show little change in mass through the incubation period.

The goals of this study were to describe the incubation behaviour of Greater Scaup in terms of incubation constancy, recess frequency and recess length, and to compare this with the behaviour of other species of ducks; further, to determine the use of endogenous reserves by Greater Scaup by examining weight loss over the incubation period; and finally, to examine intraspecific variation in incubation

constancy in terms of hypotheses regarding timing of reproduction and use of endogenous reserves.

## Methods

The study was conducted along the lower Kashunuk River drainage (61°20'N, 165°35'W) on the outer coastal fringe of the Yukon Delta National Wildlife Refuge, Alaska. The study area was described in detail by Grand *et al.* (1997). The study area was searched on foot beginning as soon as egg laying was detected, and nests were marked and mapped as described by Grand & Flint (1997).

In 1999, incubation behaviour was monitored using artificial eggs with internal thermistor probes attached to a single channel data logger, similar to those described by Flint & MacCluskie (1995). The artificial eggs were placed in the nests when the nest was found, usually during laying, and the nest temperature ( $\pm 0.2$  °C) was recorded every five minutes. All data prior to and including the day the last egg was laid were excluded from the incubation period analyses.

Incubation recesses were defined as beginning at any time the nest temperature declined by  $>2.5$  °C in three successive temperature records (elapsed time 15 minutes) and the recess ended when the temperature began to increase. To account for egg rolling and short standing breaks, any breaks when the minimum temperature was more than the mean incubation tem-

perature (calculated for each nest) minus the standard deviation divided by 1.5, or if the maximum temperature drop was less than the standard deviation divided by 1.5, were not included. Thus, breaks were defined as times when nest temperature dropped beyond the normal range of variation observed during periods when the females were on the nest. Given these criteria, nest temperature records were examined to estimate the total time spent on nests and the recess characteristics. Daily incubation constancy was calculated as the proportion of each day spent on the nest.

In a series of concurrent studies on survival and re-nesting propensity of Greater Scaup, from 1994 to 1999 females were trapped on their nests at various stages of incubation. At capture, all females were weighed to the nearest 10g. Eggs were candled to determine the stage of incubation for captured females (Weller 1956). Ambient temperatures ( $\pm 0.2^\circ\text{C}$ ) were recorded hourly at a shaded location adjacent to the study area.

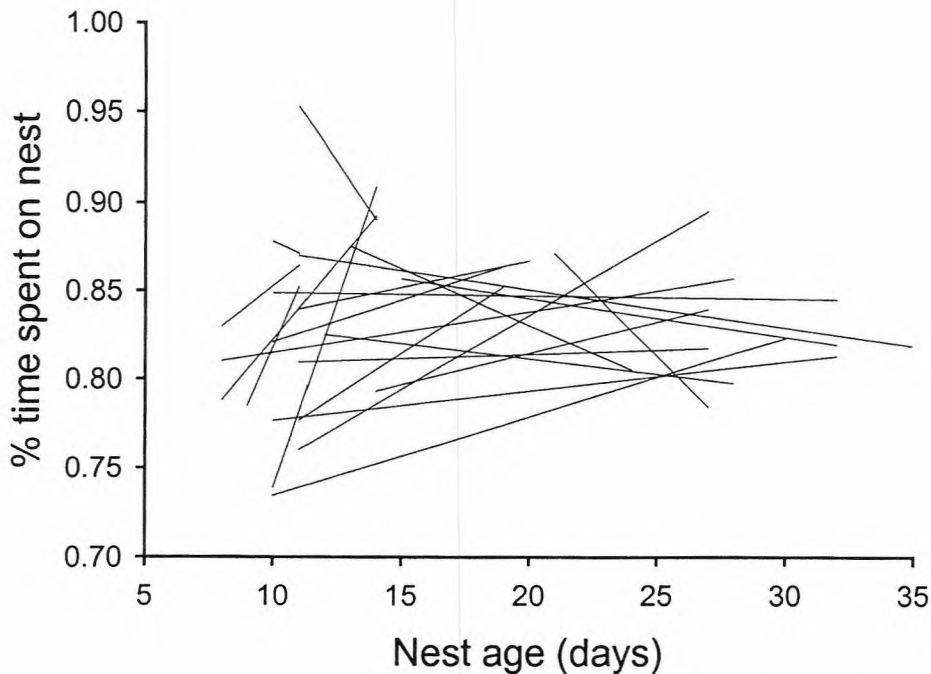
### Analyses

Analyses of covariance (ANCOVA) were used to conduct five separate analyses regarding variation in incubation parameters: (1) variation in daily incubation constancy was examined in relation to day of incubation with females as a factor and day of incubation as a covariate; (2) variation in daily recess frequency was examined with females as a factor and day of incuba-

tion as a covariate; (3) variation in length of incubation recesses was examined with females and hour as factors and ambient temperature and day of incubation as covariates; (4) variation in nest cooling during recesses was examined with females as a factor and day of incubation, recess length and ambient temperature as covariates; and (5) weight change during incubation was examined with day of incubation as a factor and year and initiation date as covariates. All first order interactions between factors and covariates were included in each of these ANCOVA analyses, but non-significant interactions were sequentially removed from the final models based on type III results. All analyses were conducted using SAS (SAS Institute 1990) and means are presented  $\pm$ S.E.

### Results

A total of 280 incubation days for 21 hens and 53 laying days for 15 hens were monitored (**Figure 1**). Incubation constancy averaged  $59 \pm 0.04\%$  during the laying period and  $83 \pm 0.01\%$  during the incubation period. The relationship between daily incubation constancy and day of incubation varied among females ( $F_{20,256}=2.30$ ,  $P<0.0016$ , **Figure 1**) and with nest initiation date ( $F_{1,256}=6.13$ ,  $P<0.0001$ ). Recess frequency averaged  $4.28 \pm 0.11$  day<sup>-1</sup> but frequency varied among females ( $F_{21,254}=4.48$ ,  $P<0.0001$ ). Average recess length was  $56.7 \pm 1.5$  minutes. Length of incubation recesses varied among females

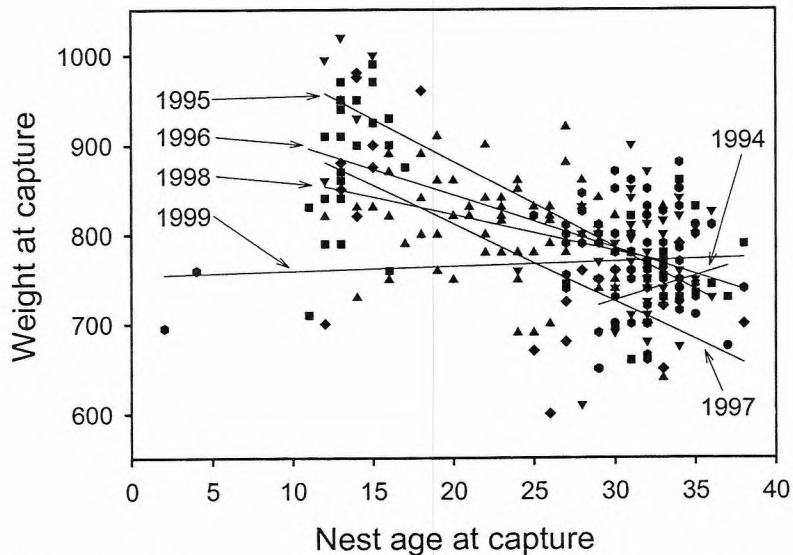


**Figure 1.** Relationships between nest age and incubation constancy for 20 Greater Scaup females on the Yukon-Kuskokwim Delta, Alaska, in 1999. Individual lines represent data for each female. Length of line indicates the number of days sampled.

( $F_{21,1116}=1.86$ ,  $P<0.01$ ). Recess length also varied with time of day, with longer breaks taken in the early morning hours; however, this relationship changed as incubation progressed ( $F_{23,1116}=1.72$ ,  $P<0.01$ ). The length of incubation recesses did not vary with ambient temperature ( $F_{1,1116}=16$ ,  $P<0.69$ ). The amount of nest cooling experienced during recesses also did not vary with ambient temperature ( $F_{1,1120}=0.29$ ,  $P<0.59$ ) but the influence of recess length on cooling varied among females ( $F_{21,1120}=15.63$ ,  $P<0.0001$ ). Ambient temperatures varied diurnally from an overnight low of

$7.4\pm 0.4$  °C to  $15.4\pm 0.4$  °C in early afternoon.

Body mass decreased with day of incubation at an average rate of  $-6.36$ g per day but the slope of this relationship varied among years ( $F_{5,250}=5.1$ ,  $P=0.0002$ , **Figure 2**) between  $+5.3$ g per day in 1996 and  $-8.0$ g per day in 1997. Body mass also decreased with initiation date at a rate of  $-4.66$ g per day ( $F_{1,250}=33.15$ ,  $P<0.0001$ ), and this pattern was consistent among years ( $F_{5,240}=0.7$ ,  $P>0.62$ ).



**Figure 2.** Relationship between hen weight at capture and nest age for Greater Scaup nesting on the Yukon-Kuskokwim Delta, Alaska. Individual lines represent regressions for each year (1994-1999). Nest age is days since the laying of the first egg. Assuming one egg laid per day, on average, incubation starts at a nest age of eight days.

## Discussion

The average incubation constancy that was measured (83%) is within the range reported by Afton & Paulus (1992) for 34 waterfowl species and is very similar to the average that they reported for Lesser Scaup *Aythya affinis*. However, this estimate is considerably lower than that for sympatric nesting Spectacled Eiders *Somateria fischeri* (90%) (Flint & Grand 1999b) and Common Eiders (96%) nesting in Maine (Korschgen 1977). Accordingly, Greater Scaup lose about 6.4g per day compared to 5.3g per day for Lesser Scaup, with both of these species losing about 20% of their initial mass (Afton & Ankney 1991). This proportional weight

loss is at the high end of the range that Afton & Paulus (1992) report for diving ducks. Consistent with interspecific variation in incubation constancy, Greater Scaup lose considerably less weight than Spectacled Eiders (16.5g day, 26% of initial mass), Common Eiders (23g per day, 33% of initial mass) or King Eiders *Somateria spectabilis* (14.8g per day, 24% of initial mass) (Korschgen 1977; Kellet & Alisauskas 1997; Flint & Grand 1999b). Overall, these data support the hypothesis that Greater Scaup rely heavily on endogenous resources to meet their energetic demands during incubation.

There was a negative relationship between nest initiation date and body weight at capture, after controlling for stage of incubation. This supports the



idea that early-nesting females are beginning incubation before adequate forage is available to meet their daily requirements. Hence, early-nesting females retain larger reserves. However, under this scenario, a concurrent negative relationship between nest attendance and stage of incubation would also be expected. These data indicate substantial among-female variation in the relationship between stage of incubation and nest attendance, with no overall pattern indicating a decline (**Figure 1**). Further, Greater Scaup lay large clutches of large eggs given their body size (Flint & Grand 1999a), making it unlikely that these clutches are produced entirely from endogenous reserves. Accordingly, in spite of the negative relationship between weight and nest initiation date, Greater Scaup do not appear to be initiating nests prior to the availability of adequate forage to meet at least a portion of their daily requirements. This is similar to the conclusion of Afton & Ankney (1991) for Lesser Scaup whereby females delay nest initiation until adequate forage is available.

Similar to the results of some other studies, there was no relationship between recess length or timing of recesses and ambient temperature (Thompson & Raveling 1987; MacCluskie & Sedinger 1999). Likewise, nest cooling was not related to ambient temperature. However, nest cooling was related to recess length, suggesting that longer recesses may be more costly in terms of egg development. While Greater and

Lesser Scaup have similar incubation constancy, Greater Scaup take about twice as many breaks of shorter duration (Afton & Paulus 1992). This difference in behaviour may be an adaptation to minimise the amount of egg cooling that occurs on a given recess because Greater Scaup nesting on the Yukon-Kuskokwim Delta are exposed to lower average ambient temperatures than Lesser Scaup nesting in Manitoba. However, individual females do not appear to alter their behaviour in relation to ambient conditions. A trade-off may therefore exist between taking longer breaks, for the female to maintain her condition, and exposing eggs to cooler temperatures, which may influence egg viability or prolong egg development time (Aldrich & Raveling 1983; Wilson & Verbeek 1995; Zicus *et al.* 1995).

Similar to the findings of Flint & Grand (1999b) and MacCluskie & Sedinger (1999), there was considerable individual variation in incubation behaviour. 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 (**Figure 1**). The patterns observed relative to day of incubation for daily incubation constancy, recess length, recess frequency and nest cooling all varied among females. Similarly, patterns of variation in mass loss during incubation varied among years. Annual and local variation in body mass dynamics have been related

to variation in forage availability (Harvey *et al.* 1989; Zicus & Riggs 1996). O'Connell (2001) documented variation in invertebrate abundance by date, among habitat types and across years on our study area. Thus, individual females are probably adapting their incubation behaviour in relation to their body condition and localised variation in forage availability. They may also be adjusting their incubation behaviour based on risk of predation or partial clutch loss. These data support MacCluskie & Sedinger's (1999) assertion that this intraspecific variation is the result of individual optimisation of incubation behaviour in relation to such factors as body condition, nest-site microclimate and available food resources.

## Acknowledgements

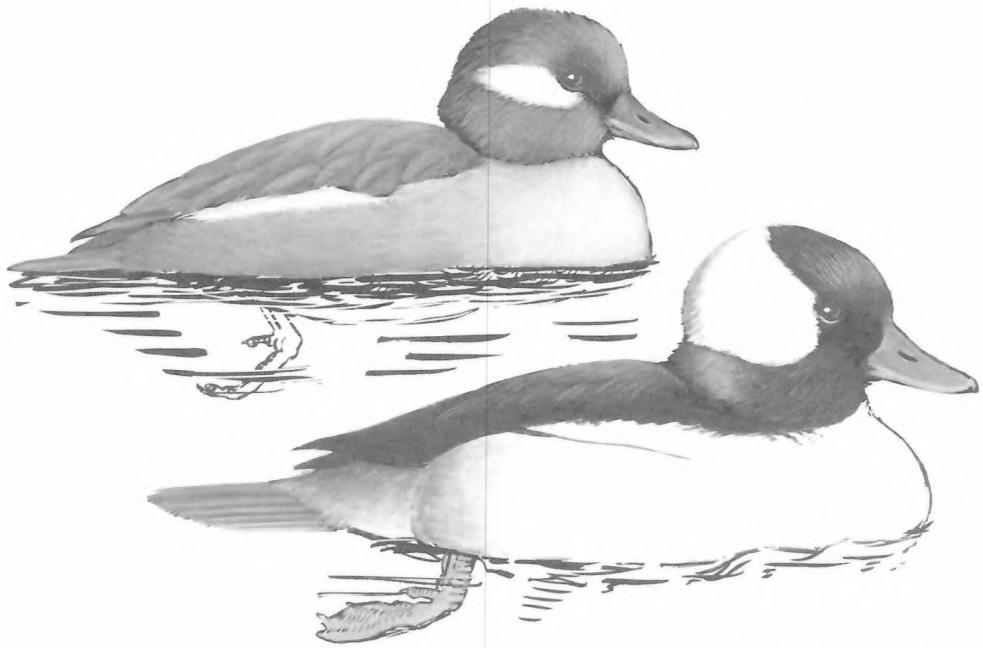
This project was funded by the Alaska Science Center, U.S. Geological Survey, and base support for the field camp was provided by R. Leedy, Migratory Bird Management, Region 7, U.S. Fish & Wildlife Service (USFWS). P.A. Liedberg, G.E. Walters and M. Rearden provided continuous support of our research. J.A. Morse assisted with field work and data analyses. G. Brewer, D.V. Derksen, J.M. Pearce, M.R. Petersen, J.A. Reed and J.L. Schamber provided helpful comments on this manuscript.

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