MOVEMENTS ON THE NEST DURING INCUBATION BY CAVITY-NESTING WATERFOWL

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We studied rates of movement on nests by wild, incubating Common Goldeneyes and Hooded Mergansers nesting in north-east Ontario in relation to ambient temperature and stage of incubation. Goldeneyes moved least frequently on the nest at all times. For both species, time intervals between movements were longer for overnight incubation sessions, and intervals remained relatively constant through incubation for morning, afternoon and overnight sessions (except for overnight sessions of Goldeneyes which increased). Our results suggest that ambient temperature influences on-nest activities of cavity-nesting ducks differently than ground-nesting species, and that there is a general relationship between body size and movements on the nest for waterfowl.

Keywords: Cavity-nesting Waterfowl, Incubation

During incubation, female waterfowl must adjust their behaviour such that their energetic requirements are met while still maintaining a suitable nest environment for the development of their eggs (Drent 1975). Females regulate the nest environment primarily by: (1) scheduling the number and duration of trips off the nest and, (2) scheduling their movements while on the nest. To date, most research on waterfowl incubation behaviour has focused on factors that influence the amount of time females spend off the nest (reviewed in Afton & Paulus 1992). However, scheduling of movements by females incubating eggs is also important for successful incubation, but has received far less attention (Afton & Paulus 1992). Movements on the nest to resettle, adjust 'tightness of sit' (White & Kinney 1974), or turn eggs are critical in promoting even heating of eggs (Drent 1975) and in preventing adhesion of developing embryonic membranes which can cause embryo mortality (Robertson 1961a, b). Most data on female movements on the nest have come from studies on ground-nesting waterfowl (eg Miller 1976, Hawkins 1986), often in semi-captive situations (eg Caldwell & Cornwell 1975, Howey et *al.* 1984). These studies demonstrate that incubating females move less when ambient temperatures are cooler, probably to minimize the chilling of eggs by regulating the frequency and intensity of contact between the female's brood patch and the eggs (eg Haftorn & Reinertsen 1982).

We address here two aspects of waterfowl incubation on species for which information is lacking. First, we describe natural rates of female movement on nests of wild, incubating Common Goldeneyes *Bucephala clangula* and Hooded Mergansers *Mergus cucullatus*. Second, we describe how females adjust these rates of movement as incubation proceeds, a topic which has received relatively little attention (see Cooper 1973, Miller 1976, Afton 1977). These species typically nest in tree cavities, incubate continuously overnight, but take several incubation recesses during the day (Mallory & Weatherhead 1993, Mallory et *al.* 1993a, Mallory & Lumsden 1994). Both species increase the amount of time spent off the nest as incubation proceeds (as do many other waterfowl), probably in response to increased ambient temperatures in boreal forest ecozones as the breeding season progresses. Based on earlier studies on semi-captive waterfowl, we expected that wild, cavity-nesting ducks would adjust movements on their nests in response to temperature. Thus, we predicted that females would move more frequently during warm daylight hours than cooler overnight hours, and that they would move more frequently later in incubation than in early incubation in response to warmer daytime and overnight temperatures.

Methods

Incubating females were monitored between 1977 and 1990 in previously established nest boxes erected on coniferous trees at edges of small lakes near Sudbury, Ontario (Mallory *et al.* 1993b) and larger lakes and rivers near Temagami, Ontario (Lumsden *et al.* 1980). The sites are situated on the Precambrian Shield within 200 km of each other, and forest cover is a mix of Great Lakes - St. Lawrence Zone and Boreal Zone. Details of study designs, nesting patterns and success are presented in Lumsden *et al.* (1980) and Mallory *et al.* (1993b).

Movements on nests by incubating females were recorded for eight Common Goldeneyes (three at Sudbury, five at Temagami, *n*=102 days, 340 incubation sessions, 5,990 movements), and four Hooded Mergansers (one at Sudbury, three at Temagami, *n*=44 days, 189 incubation sessions, 3,051 movements). Movements on nests were recorded by customized load cell incubation monitors installed in nest boxes and attached to Rustrak chart recorders (see Mallory & Weatherhead 1992). These monitors produced strip chart paper records calibrated such that 2.5 cm represented 1.0 h of incubation. Movements on nests were depicted on charts as spikes along a smooth line; thus the time between movements was determined by measuring the distance interval between spikes. For each continuous period on the nest (hereafter termed an 'incubation session'), we calculated the number of intervals, mean (± SD) interval duration, and duration of previous period off the nest. We divided incubation sessions into three periods based on our earlier observations of incubation rhythms (Mallory & Weatherhead 1992, Mallory *et al.* 1993a): (1) morning (sessions initiated after the first departure from the nest each day but prior to 12:00 EDT), (2) afternoon (sessions initiated after 12:00 EDT but before the overnight session), and (3) overnight (in all cases a single, continuous overnight session).

To examine relationships between ambient temperature and incubation patterns, we used regional air temperatures (see also Afton 1977, Mallory & Weatherhead 1993) recorded at the Sudbury airport, which was located within 50 km of all females nesting near Sudbury. We did not obtain temperature records near Temagami, but typically they are slightly lower than at Sudbury (*pers. obs.*). Incubating females could respond to several aspects of ambient temperature (eg daily maxima or minima, differences in daily extremes, overall patterns of temperature as incubation proceeds); however, we thought it conservative to use mean daily temperatures for all analyses given our lack of temperature data in close proximity to the nest boxes.

Statistical Analyses

We log transformed data on movement intervals to achieve a normal distribution for statistical tests where necessary (SAS Institute 1990). Unless otherwise noted, data are reported as mean ± SE of observed values.

We examined movements on the nest over the entire incubation period for Goldeneyes and Hooded Mergansers, which occurs between 1 May and 1 July for most females of both species. We restricted the period for analysis to days 5-29, since this time corresponds to a consistent pattern of incubation behaviour (incubation rhythm) in both species (*ie* excludes the highly variable periods at the start and end of incubation; Mallory & Weatherhead 1993, Mallory *et al.* 1993a). We used a split-plot ANCOVA to test for study site effects (accounting for repeated measures on females nested within sites and using incubation stage as a covariate). The same technique was used to test for differences due to time of day for movement intervals or their coefficients of variation among females (with time of day, species and female as main effects and incubation stage as covariate). To analyse and compare rates of movement between Common Goldeneyes and Hooded Mergansers, we performed ANCOVAs (PROC GLM), or mixed model ANCOVAs where appropriate (PROC MIXED, SAS Institute 1990), for morning, afternoon and overnight sessions, with species and female as main effects and length of sessions and incubation stage as the covariates if they were determined to be significant in earlier tests.

Results

We detected no differences in intervals of movements on nests for Goldeneyes or Hooded Mergansers between study sites (split-plot ANCOVA, F_{CG} >0.1, P>0.1, F_{HM}=2.2, P>0.1), so we pooled data for all females within each species. Based on mean values per incubation session (including all recorded sessions for all females), Goldeneyes moved 2.6 times per hour (interval 22.6 ± 0.6 min, *n*=340), and Hooded Mergansers moved 3.4 times per hour (17.4 ± 0.7 min, *n*=189). For both species, females shifted their position on the eggs most frequently in the afternoon and least frequently overnight (ANCOVAs, time of day effects, P<0.05 in both cases; **Table 1**). As well, intervals between movements were most variable during the overnight session (ANOVAs; F_{CG}=20.9, 2,307 df, P< 0.001, Tukey's test P<0.05; F_{HM}=16.7, 2,172 df, P<0.001, Tukey's P<0.05), although there were no significant differences in variation of intervals between these two species (F=0.67, P=0.41). During incubation sessions, both species also had the greatest number of movements overnight, probably because this was the longest session (**Table 1**).

After controlling for the length of incubation sessions and repeated measures on females, Common Goldeneyes moved on the nest at roughly similar intervals throughout incubation during the morning (**Figure 1** F=0.4, *n*=96, P=0.53) and afternoon (**Figure 1** F=0.01, *n*=121, P=0.92). However, Goldeneyes remained still longer between movements during each overnight session as incubation proceeded (**Figure 1** F=6.0, *n*=91, P=0.02). For overnight sessions, longer intervals between

Table 1. A comparison of the interval between movements (mean ± SE [*n*]), variation of intervals, mean number of movements per incubation session, and session length for Common Goldeneyes (*n*=8) and Hooded Mergansers (*n*=4).

	Common Goldeneye	Hooded Merganser
Interval Between Movements (min)		
Morning	19.7 ± 0.8 (109)	14.4 ± 0.5 (60)
Afternoon	17.0 ± 0.8 (129)	13.7 ± 0.5 (85)
Overnight	32.9 ± 1.3 (102)	28.6 ± 2.0 (44)
Coefficient of Variation on Intervals		
Morning	64.1 ± 1.9 (109)	60.1 ± 2.7 (60)
Afternoon	59.3 ± 1.9 (129)	59.4 ± 2.3 (85)
Overnight	75.8 ± 2.2 (102)	80.4 ± 2.5 (44)
Number of Movements per Session		
Morning	12.1 ± 0.6 (109)	11.2 ± 0.9 (60)
Afternoon	10.1 ± 0.4 (129)	12.4 ± 0.6 (85)
Overnight	33.0 ± 1.3 (102)	30.2 ± 1.6 (44)
Length of Sessions (min)		
Morning	238 ± 11 (109)	164 ± 20 (60)
Afternoon	172 ± 9 (129)	169 ± 8 (85)
Overnight	1086 ± 19 (102)	864 ± 24 (44)

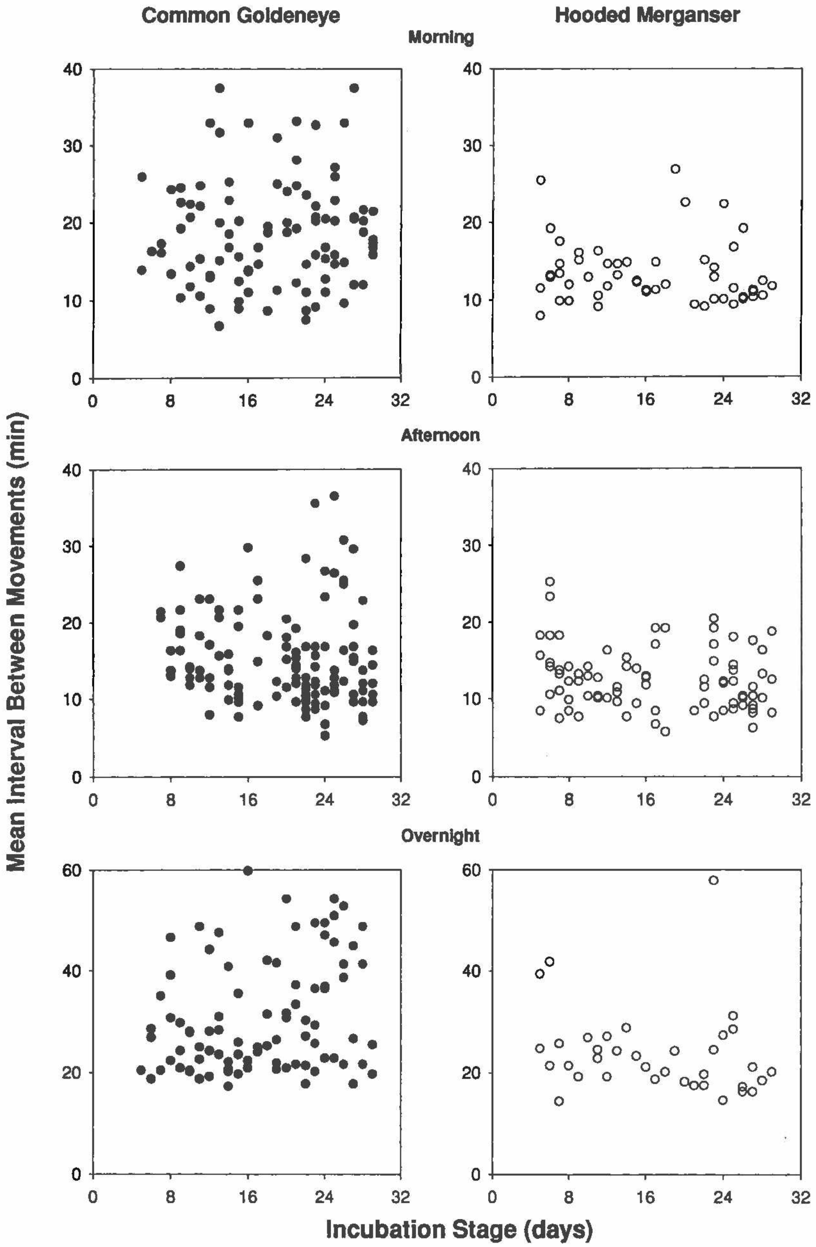

Figure 1. Patterns of movement on the nest by incubating Common Goldeneyes (*n*=8) and Hooded Mergansers (*n*=4) for morning, afternoon and overnight incubation sessions. Data are presented as means per female per day.

movements resulted in fewer movements on the nest at night (Pearson *r*= -0.85, *n*=91, *P*<0.001). Like Goldeneyes, Hooded Mergansers moved on the nest at roughly similar intervals during morning (**Figure 1** *F*=0.2, *n*=54, *P*=0.62) and afternoon sessions (**Figure 1** *F*=1.5, *n*=81, *P*=0.23) as incubation proceeded. Unlike Goldeneyes, Hooded Mergansers did not take longer intervals between movements during overnight sessions through incubation (although intervals during the last few days appeared longer; **Figure 1** *F*=0.2, *n*=38, *P*=0.70). However, Hooded Mergansers taking longer intervals between movements also moved less frequently on the nest (Pearson *r*=-0.77, *n*=38, *P*<0.001). Between 1 May and 1 July, sunrise shifts from 6:06 EDT to 5:30 EDT and sunset from 20:36 EDT to 21:25 EDT (Bishop 1994), resulting in an increase of about 1.5 hours of daylight. Despite this increase, the length of overnight incubation sessions did not vary significantly for either species (Pearson correlations, *P*>0.1 in both cases). Also, intervals between movements on the nest at all three time periods were unrelated to the length of the previous incubation recess for both species (Pearson correlations, *P*>0.1 in both cases).

For morning and afternoon sessions, Goldeneyes had significantly longer intervals between movements than Hooded Mergansers (**Table 1** morning, *F*=40.2, df 1,137, *P*<0.001; afternoon, *F*=23.1, df 1,190, *P*<0.001). For the overnight session, after controlling for the effect of incubation stage (*F*=4.8, df 1,116, *P*=0.03), Goldeneyes again took longer between movements on the nest than Hooded Mergansers (**Table 1** *F*=15.6, df 1,116, *P*<0.001). After controlling for session length and female, Goldeneyes and Hooded Mergansers made similar numbers of movements during morning sessions (**Table 1** ANCOVA, *P*=0.9). However, Hooded Mergansers made more movements during afternoon sessions than Goldeneyes (**Table 1** *F*=34.0, df 1,190, *P*<0.001), while Goldeneyes made more movements during overnight incubation sessions (**Table 1** *F*=5.0, df 1,116, *P*=0.03).

In north-east Ontario, mean daily temperatures between 1 May (6.3°C) and 1 July (15.6°C) increase significantly (10 year mean values; r_s=0.70, *n*=62, *P*<0.001). In 1989 and 1990, the period for the most recent monitoring records, the differences in mean daily temperatures between 1 May and 1 July were 16.3 and 13.9°C respectively, and the mean daily difference in temperature (*ie* minimum to maximum) over this 62 day time period was 11.1 ± 0.2 °C. Thus, there was a substantial daily and seasonal change in ambient temperatures to which nesting females may have adjusted their movements. In support of this contention, overnight movements tended to occur at longer intervals when mean daily temperature was higher for the Goldeneye monitored for the most complete incubation period at Sudbury in 1990 (**Figure 2**; ANCOVA on log-transformed data controlling for incubation stage, *F*=7.4, df 2,20, *P*=0.07).

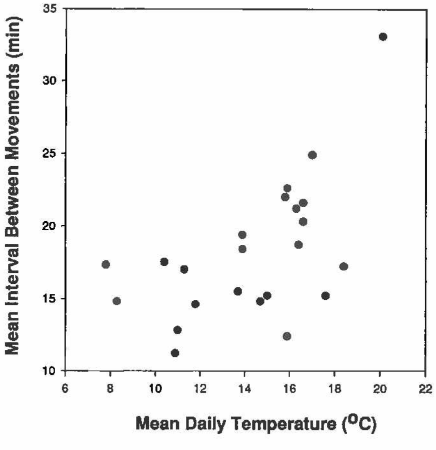

Figure 2. Relationship between overnight movement intervals and mean daily temperature for one female Common Goldeneye monitored in 1990 for which we had the most complete set of data. After controlling for the effect of incubation stage, overnight movements tended to occur at longer intervals when mean daily temperature was higher (ANCOVA, *F*=7.4, df 2,20, *P*=0.07).

Table 2. Rates of movement on the nest for waterfowl species. Female masses are from Afton & Paulus (1992). Note that methods for determining rates of movement differed between studies, as did number of parents, environment, and mean clutch size.

SPECIES	Rate of Movement (moves/hr)	Body Mass (g)	Reference
Whooper Swan *Cygnus cygnus*	0.9[1]	8100	Howey *et al.* 1984
Whistling Swan *Cygnus columbianus columbianus*	2.2-3.2	6300	Hawkins 1986
Bewick's Swan *Cygnus columbianus bewickii*	3.3	5700[2]	Evans 1975
Black Swan *Cygnus atratus*	1.0[1]	5000[2]	Howey *et al.* 1984
Giant Canada Goose *Branta canadensis*	1.4	4628	Cooper 1973
Barnacle Goose *Branta leucopsis*	1.3[1]	2020	Howey *et al.* 1984
Common Merganser *Mergus merganser*	4.3	1076	Mallory unpublished
Mallard *Anas platyrhynchos*	1.6-2.1	1047	Caldwell and Cornwell 1975
Common Goldeneye *Bucephala clangula*	2.6	687	This study
Northern Shoveler *Anas clypeata*	2.3	569	Afton 1977
Hooded Merganser *Mergus cucullatus*	3.4	536	This study
Blue-winged Teal *Anas cyanoptera*	6.2	356	Miller 1976

[1] Calculated from figures in (Howey *et al.* 1984); reported rates for egg-turning are lower (Howey *et al.* 1984)

[2] Masses from Wilmore (1974)

Discussion

Incubating female Common Goldeneyes and Hooded Mergansers moved at longer intervals during overnight incubation sessions than during daytime incubation sessions, probably in response to cooler night-time ambient temperatures. Thus, our results for wild, cavity-nesting ducks support Caldwell & Cornwell (1975) and Afton (1977) who reported similar findings on semi-captive Mallards *Anas platyrhynchos* and Northern Shovelers *Anas clypeata*. However, we found that females did not move in shorter intervals as incubation proceeded; in fact, female Goldeneyes increased the interval between movements through incubation during overnight sessions, despite the fact that daily temperatures increase substantially over the incubation period. This result is contrary to Caldwell & Cornwell (1975) and Miller (1976), who found that female Mallards and female Blue-winged Teal *A. discors* respectively, moved more frequently as ambient temperatures increased through incubation. One possible explanation is that nests in cavities may not fluctuate in temperature as much as ground nests because they are more sheltered from convective heat loss due to wind, although this hypothesis has received little attention (Wilson & Verbeek 1995). This effect can significantly increase egg cooling within and between nests of ground-nesting waterfowl species (Howey *et al.* 1984, Thompson & Raveling 1988). Thus, the microclimate in nest cavities may be less variable than ground nests, requiring less adjustment in incubation behaviours such as movements on the nest by the female to reheat eggs. At present, there are insufficient data on interspecific rates of nest and egg cooling to assess this hypothesis (Afton & Paulus 1992). Nonetheless, our result that movement intervals were unrelated to the duration of the previous incubation recess (hence degree of egg cooling) for two cavity-nesting species is consistent with this hypothesis. Collectively, our results and those of previous studies suggest that ambient temperature influences the rate of movement on the nest of incubating female waterfowl, but perhaps not as strongly for cavity-nesters as for ground-nesters. Moreover, the influence may not be as strong as the role temperature plays in the timing of recesses off the nest (Afton & Paulus 1992).

We found that Common Goldeneyes took the longest intervals to shift positions at all times. Afton & Paulus (1992) demonstrated that waterfowl incubation behaviour follows a general relationship whereby larger species tend to have higher nest attentiveness. For those species for which data on movement intervals are known (**Table 2**), larger swans appear to have less frequent movement intervals than smaller ducks. This suggests that behaviour during incubation sessions may follow a similar relationship as is found for nest attentiveness among waterfowl. However, the patterns suggested in **Table 2** must be interpreted cautiously, since the species and studies cited differ in the number of parents involved in incubation, the mean clutch size, the environment of the study, and the types of movements included in the reported rates (egg-turning, comfort movements, adjusting tightness of sit). As suggested by Afton & Paulus (1992), relatively little is known about the behaviour of waterfowl on the nest, and thus further investigation is warranted, particularly in regards to interspecific variation in movement rates.

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