EGG-LAYING TIME AND LAYING INTERVAL IN THE COMMON EIDER[1]

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Abstract. We determined the time of day at which eggs were laid and the laying interval (time between laying of successive eggs in a clutch) in the Hudson Bay race of the Common Eider (*Somateria mollissima sedentaria*), at La Pérouse Bay, Churchill, Manitoba (58°24′N, 94°24′W). Nests were found at the one-egg stage and were subsequently visited three times daily. Analysis of the nest contents at each visit allowed us to estimate mean egg-laying times as well as the mean time at which eggs were lost to predators. The estimated mean egg-laying hour was 13:49 (CST, 95% CL 12:30–15:06). We detected no selective advantage to laying at this time based on the timing of egg predation. The average egg-laying interval was 27.7 ± 3.4 hr. Laying intervals decreased with increasing clutch sizes. For clutches of four and five eggs, the estimated interval between the last two eggs was significantly longer than that for intervals between all other eggs, all other comparisons between intervals were not significantly different. If last-laid eggs were excluded the mean laying interval for all eggs was 26.1 ± 4.3 hr, confirming that the last egg in a clutch takes longer to produce. We suggest that longer laying intervals of last-laid eggs may be related to hormonal changes associated with the onset of incubation.

Key words: Common Eider; Somateria mollissima; *egg-laying interval; egg-laying time; predation.*

INTRODUCTION

Timing of breeding and the duration of the breeding period are important factors affecting reproductive success in birds (Daan et al. 1988). These factors are determined, in part, by the egg-laying interval: the time between the laying of successive eggs in a clutch. The length of the laying interval could affect individual fitness in a number of ways, for example due to increased vulnerability of nest contents to predation (Clark and Wilson 1981), declining viability of unincubated eggs (Arnold et al. 1987), seasonal declining food availability (Bryant 1975) and delay in the timing of hatching (Cooke et al. 1984). Under conditions which favor a shortened and/or earlier breeding period, laying interval should be under directional selection to become shorter until such time that counter-selectional forces lead to stabilizing selection. A decrease in the length of the laying period may be achieved by shortening the laying interval, by reducing the clutch size, or both. A decrease in clutch size has obvious fitness disadvantages, so there may be stronger selection to shorten the laying interval. Decreasing the clutch size may, however, be beneficial where pre-incubation nest predation is high

(Lack 1947). Evidence of shorter incubation periods in more northerly nesting geese, which are subject to a relatively short summer (Johnsgard 1968, Ogilvie 1978, Owen 1980, Thompson and Raveling 1987), supports the hypothesis that selection for shortening the breeding period does occur.

The egg-laying interval may also be influenced by selection to lay at a particular time of the day. Egg-laying time may be controlled by a number of factors including photoperiod (Johnson 1986), egg fragility (Schifferli 1979, but see Weatherhead et al. 1991), or circadian patterns in activities such as ovulation, copulation, fertilization (Weatherhead et al. 1991), feeding, or predation. Strong selection for laying at a particular time of the day should result in low variation in individual egg-laying times.

Despite the evolutionary and ecological importance of laying interval and laying time to reproductive success, these factors have been poorly studied in wild birds (Cooper 1978; Weatherhead et al. 1991; Ankney and Alisauskas 1992; Schubert and Cooke, in press). Although most studies are consistent with the hypothesis of a constant 24-hr laying interval, with eggs laid early in the morning, data support alternative hypotheses equally well (Schubert 1990). Furthermore, most published information on egg-laying intervals has been collected anecdotally or

incidentally and few studies have included multiple daily nest visits. In addition, confounding factors such as intraspecific nest parasitism (where two females lay in a single nest but only one incubates) and undetected egg predation have seldom been considered, even though these may significantly affect estimates of laying intervals.

The aims of this paper are (1) to estimate egg-laying times and laying intervals based on multiple daily nest visits, (2) to determine if and how these vary with clutch size and position of eggs in the laying sequence, and (3) to investigate whether variation in probability of predation throughout the day acts as a selective force influencing egg-laying times in the Hudson Bay race of the Common Eider (*Somateria mollissima sedentaria*). Three characteristics of this subspecies suggest that there should be strong selection to shorten both the breeding period in general and, more specifically, the laying interval. First, pre-incubation nest predation is high (Choate 1967, Guild 1974, Schamel 1977, Robertson and Cooke 1993). Second, energy for egg production and incubation is derived largely, if not solely, from nutrients acquired before laying begins (Parker and Holm 1990). Hence, female Common Eiders require little time for foraging during laying and incubation (Cooch 1965, Johnsgard 1968, Milne 1976, Korschgen 1977, Parker and Holm 1990). Finally, Hudson Bay Common Eiders live in Arctic regions year-round and thus are subject to both a short breeding season as well as a harsh winter, which should select for a rapid breeding cycle.

STUDY AREA AND METHODS

STUDY AREA AND FIELD METHODS

Field work was carried out at La Pérouse Bay, Manitoba (58°24′N, 94°24′W) in 1991. The study area comprised part of the Mast River Delta where a large colony of Common Eiders nests on the ground on fresh water islands. The major predator of eggs in this area are Herring Gulls (*Larus argentatus*), other predators include Arctic Foxes (*Alopex lagopus*), Northern Ravens (*Corvus corax*), and Parasitic Jaegers (*Stercorarius parasiticus*). Due to the deep water surrounding the nesting islands at egg-laying we believe most predation was by avian predators. Schmutz et al. (1983) describe the study site and Freemark (1977) gives a detailed description of the vegetation. We searched the study area for newly-initiated nests three times daily from 27 May (when we found the first egg) until 4 June, and once per day from 5 to 9 June. Nests were found by visually searching nesting islands for covered eggs. Although first eggs are covered by nesting materials and are certainly not obvious to a casual observer, we (MDW and GJR) have had prior experience in searching for nests in this environment and experienced no problem finding new nests. Once found, nests were visited three times daily until 7 June, and twice on 8 June. The timing of nest visits throughout the day were approximately 05:00 to 11:00 (MDW), 12:00 to 18:00 (GJR) and 20:00 to 23:00 (MDW and GJR). The daylight period at this time of the year was approximately 03:00 to 22:30 (all times are given in Central Standard Time). Nests at which eggs were laid on 7 or 8 June were visited once more in the following week. Nests in which new eggs were found at that time were excluded from any analyses that required knowledge of laying times for all eggs in the clutch. Nests were marked with small, numbered wooden sticks. At each visit the time was recorded to the nearest minute. Newly found eggs were numbered according to laying sequence, and the status of each previously laid egg was recorded (e.g., present, missing or depredated). For each new egg, fresh mass (±1 g) was recorded with a 300 g Pesola spring balance, length and maximum breadth were measured with vernier calipers (±0.1 mm), and egg color was scored by visually matching the egg with colored paint chips. We estimated the time at which a nest site was searched prior to laying of the first egg by interpolating from the times when surrounding nests already containing eggs were visited; these estimates are accurate to within about 20 min. We attempted to minimize the time we spent at each nest, and the nest was covered with material after the visit, which substantially reduces predation rates (Götmark and Ahlund 1984). In addition, gulls in the local area tended not to follow us, they seemed more concerned with attending their nests while we were in an area. Females that were flushed generally returned to their nests within 5 min of the nest visit. We also approached attending females very slowly so that they would not flush but rather just walk from their nests into the water. Flushed females generally watched our activities from a safe distance (about 25 m) and used the opportunity to preen and drink.

Intraspecific nest parasitism confounds the determination of egg-laying patterns in this popu-

lation. In the 1991 breeding season an estimated 42.4% of all nests that survived to incubation contained at least one parasitic egg (see Robertson et al. 1992 for details of the methods used to identify parasitic eggs). Parasitic eggs were excluded from clutches and remaining eggs were renumbered to reflect their true position in the laying sequence. Only nests found at the one-egg stage were included in the analyses. Additionally, if two or more days passed between the finding of new eggs in a nest and these new eggs were different in terms of size and color of the original clutch; we assumed that these eggs were laid by a second female and renumbered the new eggs accordingly.

ESTIMATING EGG-LAYING TIMES

The following method was used to estimate the number of eggs laid during each hourly interval of the day from the nest information collected three times daily. We estimated the probability that an egg had been laid in each interval by conservatively assuming that there was a constant probability of egg-laying throughout the interval between nest visits just prior to an egg being found. For example, if an egg was found at 20:00 and the previous nest visit had been 15:00, the probability of the egg being laid in each hourly interval between 15:00 and 20:00 was 0.2. For all other hourly intervals of the day the probability was zero. The process was repeated for all eggs and the probabilities for each hourly interval were summed to give an estimate of the total number of eggs laid for each hour of the day. Circular statistics were used to analyze data concerning daily activity patterns: the Rayleigh Test detects unimodal deviations from random distributions of activity during the day and the Watson and Williams test compares the mean times of two distributions (Brown and Downhower 1988). For both of these tests, the eggs for each hourly interval were assumed to have been laid on the half hour. The method for determining the mean time of a group of events is given by Brown and Downhower (1988) and 95% confidence limits for estimated mean times were calculated following Zar (1984, p. 665).

ESTIMATING EGG-LAYING INTERVALS

The maximum and minimum mean laying intervals for a particular clutch were estimated (assuming a constant laying interval) by the equations:

$$maximum = \frac{[time(last\ egg\ found) - time(visit\ before\ egg\ 1\ found)]}{(clutch\ size - 1)}$$

$$minimum = \frac{[time(visit\ before\ last\ egg\ found) - time(egg\ 1\ found)]}{(clutch\ size - 1)}$$

The mean laying interval was estimated as the mean of the maximum and minimum values. The analysis was repeated excluding the last egg in each clutch to determine if the interval between the penultimate and the ultimate egg in a clutch was longer than the average interval between consecutive pairs of earlier eggs. To determine the laying interval for each position in the laying sequence, we estimated time of laying as the midpoint between the time of the nest visit preceding that at which the egg was found and the time at which it was actually found. The between-egg interval was then estimated as the time between any two estimated egg-laying times. This analysis was repeated for clutches of 3–5 eggs and for each interval in the laying sequence.

TIMING OF EGG PREDATION

In this analysis we included all eggs that had been marked but later disappeared or were found destroyed at a nest before the full clutch had been laid. The method used to estimate egg predation times during the day was identical to that used to estimate the time that eggs were laid. Two probability distributions were generated: (1) the temporal distribution of individual egg depredations, and (2) the distribution of predation events. These distributions differed because although predators generally take single eggs, in some cases more than one egg went missing or was destroyed between a single pair of nest visits. We assumed that all depredated eggs had been taken by a single predator during a single predation event in the second analysis and therefore treated losses of multiple predated as a single data point. In order to determine whether or not predation pressure may be influencing the evolution of egg-laying times, we assumed that the presence of females in the vicinity of a nest increased the probability of nest detection by predators (although if the female is on her nest she can defend her eggs, it is when she leaves the nest that she gives away the location of her eggs) and that the degree of activity at the nest for each hour of the day was accurately represented by the estimated number of eggs laid. For each hour-
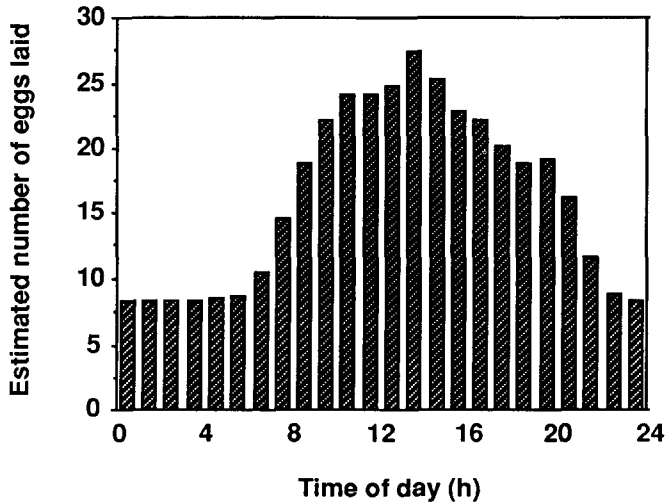
FIGURE 1. Estimated distribution of egg-laying times.

ly interval of the day, two estimates of predation pressure were calculated as follows:

$$\text{predation pressure}_1 = \frac{\text{estimated \# eggs depredated}}{\text{estimated \# eggs laid}}$$

$$\text{predation pressure}_2 = \frac{\text{estimated \# predation events}}{\text{estimated \# eggs laid}}$$

If predation pressure is uniform throughout the day, these distributions are expected to be well estimated by linear relationships with slopes of zero.

RESULTS

CIRCADIAN PATTERNS OF ACTIVITY

The distribution of egg-laying times was significantly different from uniform ($w = 32.2$, $n = 390$, $P < 0.05$, Fig. 1) and the mean estimated egg-laying time was 13:49 (95% CL 12:30–15:

06). The mean estimated laying time for each clutch size and laying sequence are presented in Table 1. Early sequence eggs are laid around noon and are progressively laid later in the day as the clutch progresses, there appears to be no difference among clutch sizes as most 95% confidence limits overlap. The timing of nest visits may have biased our estimates of mean laying times. In order to determine the extent of this bias, we simulated the method used to generate estimated laying time distributions using predicted egg-laying times. The results indicate that for eggs laid between 13:00 and 14:00, the maximum difference between the true time of egg-laying and the predicted time of mean egg-laying was 0.35 hr.

Both the distribution of estimated number of eggs preyed upon and the distribution of estimated number of predation events were nonuniformly distributed throughout the day ($w = 8.8$, $n = 128$ eggs, $P < 0.05$ and $w = 6.0$, $n = 101$ events, $P < 0.05$ respectively, Fig. 2). The

TABLE 1. Estimated egg-laying times (mean CST ± 95% CL) for female Common Eiders according to clutch size and laying sequence. Distributions that were not different from random (i.e., means are not relevant) are denoted non-significant (NS). Samples sizes for clutches 3 to 5 are 15, 20 and 26.

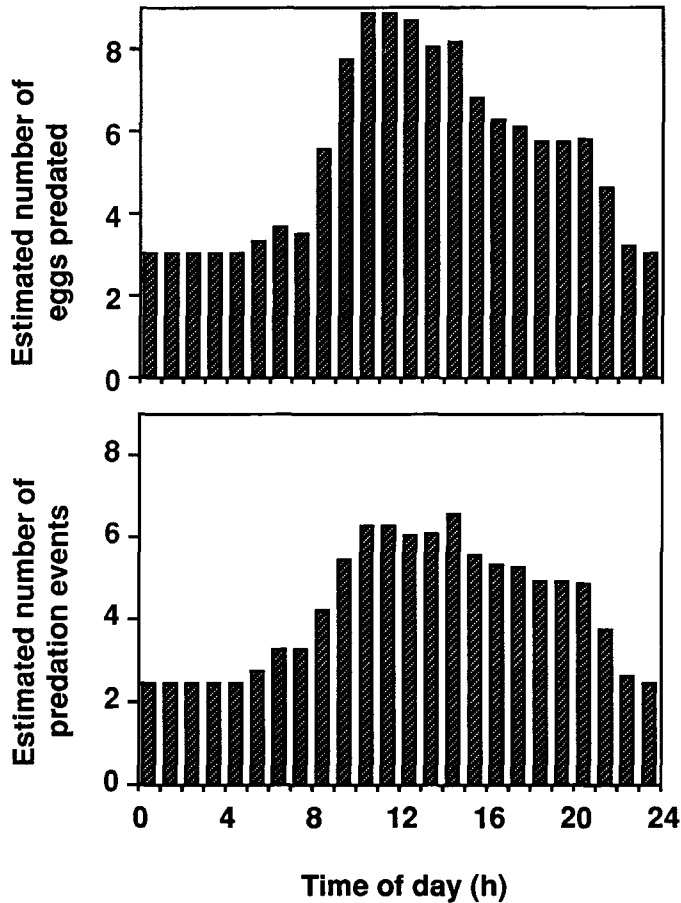| Clutch size	Laying sequence				
	1	2	3	4	5
3	14:16 ± 2:32	17:38 ± 3:36	00:16 (NS)		
4	12:51 ± 1:12	15:10 ± 2:28	13:28 ± 3:24	18:23 ± 3:44	
5	13:15 ± 3:20	11:35 ± 2:12	11:31 ± 2:00	12:01 ± 1:32	16:49 ± 1:44

FIGURE 2. Estimated distribution of egg predation times and egg predation event times.

mean estimated times of egg predation and egg predation events were 13:38 (95% CL 12:06–15:06, maximum bias = 0.35 hr) and 14:05 (95% CL 11:48–16:24, maximum bias = 1.65 hr) respectively. The mean times of these two distributions were not significantly different ($F = 0.14$, df = 1.227, $P > 0.05$). The relationship between predation pressure$_1$ and time of day was better estimated by a linear than a quadratic equation and indicates that predation pressure$_1$ was nearly uniform throughout the day (product-moment correlation, $r = 0.26$, df = 22, $P > 0.05$, Fig. 3). The relationship between predation pressure$_2$ and time of day, however, was significantly estimated by a second order polynomial equation ($r = 0.54$, df = 22, $P < 0.01$, Fig 3). The distribution indicates that predation pressure$_2$, the ratio of estimated number of predation events to estimated

number of eggs laid, may have been slightly lower at midday than in the early morning or in the course of the evening.

LAYING INTERVALS

The mean clutch size (± 1 SD) was 4.42 ± 1.17 (Robertson et al. 1992). The mean laying interval was 27.7 ± 3.4 hr ($n = 87$ clutches) for all eggs in the clutch. When the last-laid egg in each clutch was excluded from calculations, the average laying interval was shorter (26.1 ± 4.3 hr, $n = 82$ clutches). For clutches of four and five eggs, the estimated interval between the last two eggs was significantly longer than intervals between all other eggs, all other comparisons were insignificant (analysis of variance [ANOVA] followed by Tukey's test for clutches of four, $F = 6.50$, df = 2, 80, $P = 0.0024$, for clutches of five, $F =$
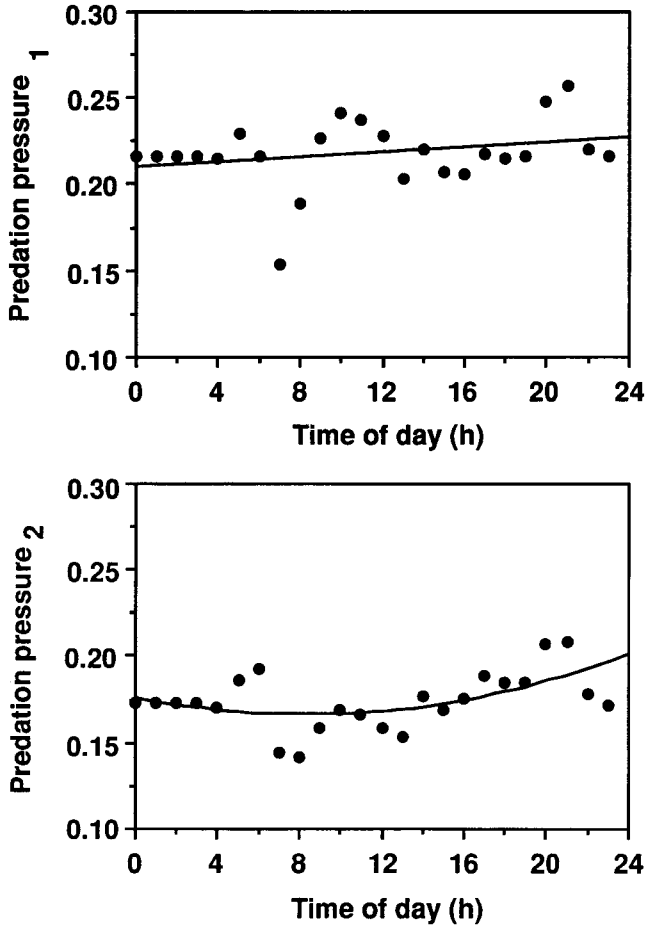
FIGURE 3.   Two measurements of predation pressure with respect to time of day. Predation pressure$_1$ is based on losses of individual eggs, predation pressure$_2$ is based on the number of unique predation events (see text for additional details). The relationship between predation pressure$_1$ and time of day is best estimated by the equation y = 0.21 + 0.001x. The relationship between predation pressure$_2$ and time of day is best estimated by the equation y = 0.18 + 0.002x + 0.0001x^2.

16.23, df = 3, 131, P = 0.0001, Fig. 4). The trend was similar for clutches of three, although the difference is not significant (ANOVA, F = 1.82, df = 1, 44, P = 0.18, Fig. 4). Clutch sizes of three had the longest laying intervals followed by clutches of four, clutches of five had the shortest laying intervals (ANOVA, F = 12.53, df = 2, 255, P = 0.0001, Fig. 4) when pooled over all sequences.

DISCUSSION

A major criticism of many previous studies of egg-laying in wild birds is that infrequent nest visits, often combined with small sample sizes, provide inadequate information to accurately

determine laying times or intervals (Schubert 1990). In this study, multiple daily visits of a large number of nests allowed for more accurate estimation of egg-laying times and of variation within the population. In addition, we were able to control for the effects of intraspecific nest parasitism and egg predation that may have confounded estimates of egg-laying intervals.

The method we used to estimate the number of eggs laid during each hour of the day was conservative, such that the true peak in egg-laying times was expected to be greater than the one we estimated. Nevertheless, we demonstrated a strong midday peak in egg-laying times in this population of Common Eiders. In contrast to this
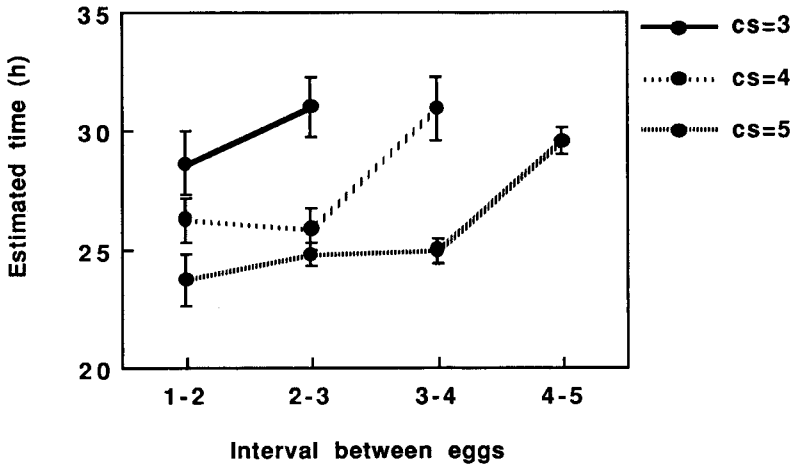
FIGURE 4. Estimated average between egg intervals (with SE bars) for clutches of three, four and five eggs.

result, it has been traditionally assumed that waterfowl lay their eggs in the early morning hours (Johnsgard 1968). Some studies support this generalization. For example, Oring (1969) observed that Gadwall (*Anas strepera*) eggs were laid before noon, and Duebbert (1966) indicated that most female Gadwalls visit their nests to lay eggs between 05:00 and 07:00. Other species of waterfowl, however, are thought to lay at non-diel intervals, suggesting that eggs are laid throughout the day (for example, Black Swan, *Cygnus atrata* [Kear 1972], Magpie Goose, *Anseranas semipalmata* [Johnsgard 1961], Canada Goose, *Branta canadensis* [Cooper 1978] and Lesser Snow Goose, *Anser caerulescens caerulescens* [Schubert and Cooke, in press]). Regardless of the situation in other populations, however, it is interesting to consider the potential adaptive basis for this population's hour of laying.

We were unable to detect a strong selective advantage to laying around midday based on the timing of predation. Although, the timing of predation reflected the timing of laying, this does truly represent predation pressure. Laying at a particular time of the day would be advantageous if individuals laid their eggs at an hour when the probability of predation was low, and relatively low values of predation pressure around midday would suggest an explanation for the observed midday peak in laying times. Although the ratio of estimated number of predation events to number of eggs laid appears to be slightly lower at midday than at any other time, the distribution of the ratio of estimated number of eggs depre-

dated to number of eggs laid showed no such trend. The estimated number of eggs depredated may be an inappropriately inflated sample of the estimated number of predation events. Alternatively, number of eggs depredated may be a better measure of the selective pressure acting on egg-laying times because it compares two values with the common currency of individual eggs. Convincing evidence of the adaptive significance of egg-laying times with respect to timing of predation was not found because of this discrepancy in our results, but the selective pressure due to predation is clearly not very strong. It could be that Eiders and their egg predators are both more active around midday, and they are not influencing each others activities.

There are several reasons why we may not have detected a selective advantage to laying around midday. First, the evolution of egg-laying times may not be influenced by the timing of predation. Second, the predation data may be biased by the fact that eggs preyed upon shortly after being laid are those most likely to be undetected by the observer. However, this hypothesis assumes that predators use the presence of females (i.e., just after she leaves the nest) to aid in nest detection. If this is the case then most predation occurs shortly after eggs were laid, while the probability of female presence at the nest was relatively high. Third, the absolute and relative numbers of predators may vary greatly among years (Matthew Collins, pers. comm.), so it is possible that similar analyses performed on data for a different year would have given different

results. With the data available, it is possible only to speculate on the potential effect of predation pressure on egg-laying times.

It is possible that individuals in this population benefit from laying synchronously, rather than around midday per se. The distribution of nests in this population is more clumped than the distribution of suitable nesting habitat, suggesting that Common Eiders in this population may benefit in some way from coloniality, perhaps because of group defense against predators or advanced warning through communication of an approaching predator (Schmutz et al. 1983). Temporal synchrony in the hour of egg-laying might reduce egg predation through predator swamping, if predators use the presence of females leaving their nests to find eggs. In a population of Common Eiders nesting in Europe, females lay their eggs very early in the morning (Myrfyn Owen, pers. comm.). Drift in the mean laying time among populations is expected if benefits result from laying synchronously rather than at a particular time of day. The actual distribution of egg-laying times probably has a lower variance than the distribution estimated by our method. Some eggs (a maximum of 13%), however, were laid between 23:00 and 05:00, suggesting that no single environmental cue is responsible for egg-laying times in all individuals.

The laying intervals were longer in small clutches (three eggs) and shortened in larger clutches (five eggs). Young Eiders and Eiders in poor condition are known to lay later in the season (Spurr and Milne 1976), also clutch size decreases over the season (Robertson et al. 1992). Therefore, these young birds or birds in poor condition, that lay small clutches, could also be taking longer to lay their eggs, and the converse could be true for Eiders in good condition. Egg size does not vary with clutch size in this population (Robertson and Cooke 1993). So eggs from smaller clutches are not larger, which may make them longer to lay. An alternative explanation is that birds that are going to lay larger clutches somehow decrease their laying intervals because their laying period is already going to be long. In addition, undetected predation and/or nest parasitism could effect the relationship between laying intervals and clutch size.

Selection may act more strongly on laying intervals than on laying times. If so, egg-laying time may be constrained by the laying interval, rather

than the other way around. We estimated the mean laying interval for all eggs in a clutch as 27.7 ± 3.4 hr. The inability to determine laying intervals accurately when nests are visited infrequently may account for the discrepancy between our result and the 24 hr interval generally reported for the Common Eider in studies which focus on other aspects of their breeding biology (Paynter 1951, Cooch 1965, Milne 1974, Schmutz et al. 1983).

When the last egg laid in each clutch was excluded, the mean laying interval was shorter (26.1 $\pm$ 4.3 hr), indicating that the interval between the penultimate and ultimate egg may be longer than the intervals between other pairs of eggs in a clutch. This result is supported by significantly longer intervals between the last two eggs in clutches of four and five. Longer laying intervals for last eggs have been reported for several other bird species including the Prairie Warbler, *Dendroica discolor* (Nolan 1978), the European Starling, *Sturnus vulgaris* (Meijer 1992) and the Lesser Snow Goose (Schubert and Cooke, in press). Although later eggs in Prairie Warbler clutches were larger than others (Nolan 1978), and mean egg-weight was positively correlated with laying interval in the European Starling (Meijer 1992), this was not the case in precocial Lesser Snow Geese (Schubert and Cooke, in press). In this population of Common Eiders, last eggs in a clutch are smaller than all others (Robertson and Cooke 1993). A similar trend has been demonstrated for other precocial species, for example, Canada Goose, *Branta canadensis* (Leblanc 1987), American Coot, *Fulica americana* (Arnold 1991), and Lesser Snow Goose (Williams et al. 1993) clutches. Leblanc (1987) suggested that smaller last eggs in Canada Goose clutches, where incubation begins before the last egg is laid, may be the result of high prolactin levels associated with onset of incubation. In American Coots, Arnold (1991) similarly showed a relationship between decreasing egg size at the end of a clutch, and the number of follicles that were simultaneously developing. He suggested that the process of decreasing yolk deposition and the suppression of developing additional follicles may be regulated by the same hormonal mechanisms. In American Coots, incubation started between the laying of eggs three and six in that population and the volume of eggs started to decrease slowly beginning with third to fifth eggs (Arnold 1991). Furthermore, in Prairie Warblers, last eggs were

laid later in the day only when females roosted on their nest the night before laying the last egg (Nolan 1978), perhaps because physical contact with eggs stimulates prolactin release (e.g., Hall 1987), possibly inhibiting development of the last egg. In Common Eiders, females generally begin incubating after laying the penultimate egg (Cooch 1965), suggesting that hormonal changes associated with incubation occur before the last egg is fully developed (Goldsmith 1990). We extend the hypothesis put forward by Leblanc and supported by Arnold by suggesting that these same hormonal mechanisms may be responsible for the observed decrease in the rate of egg production and therefore an increase in laying interval for last-laid eggs in the Common Eider.

ACKNOWLEDGMENTS

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