Wilson Bull., 105(3), 1993, pp. 414–426

EGG-LAYING INTERVALS IN THE LESSER SNOW GOOSE

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ABSTRACT.—The laying interval for Lesser Snow Geese (*Chen c. caerulescens*) at La Pérouse Bay, Manitoba, calculated using two separate approaches, was approximately 33 ± 3 h. This value conflicts with the estimate of a 24 h interval suggested by Cooch (1958). The contradiction is probably due to methods of data collection. Neither egg size nor female age affected laying interval. There was no correlation between weather conditions and laying interval. Significant but small differences in mean laying interval between years were found, with a mean lying between 31 and 35 h. *Received 17 Aug. 1992, accepted 23 Feb. 1993.*

In birds, the amount of time between the deposition of successive eggs (laying interval), which ultimately determines time required to complete a clutch (laying period), is one factor affecting time of year when young hatch. Given equal nest-building and incubation periods, a shorter or longer laying interval could result in young of one individual hatching in a more favorable environment than young of another. Therefore, laying interval is an important avian trait that is susceptible to natural selection. Time of day at which an egg is laid (laying time) can also affect laying interval. If it is beneficial to lay at approximately the same time every day, the laying interval should be approximately 24 h or a multiple thereof. For instance, birds may tend to lay in the morning because this helps to prevent breakage of eggs in the oviduct (Schifferli 1979). Alternatively, laying early in the day may allow females to perform daily activities such as feeding or nest defense without being hindered by the weight of an egg in the uterus (O'Connor 1984). If there is no timing restriction, however, or if variable laying times are advantageous, laying intervals could be any length and could be equal between all eggs (constant) or longer between some eggs than others (variable). In order to study laying interval properly, therefore, we must also investigate laying time.

Because laying interval is susceptible to natural selection, there must be advantages and disadvantages to shorter or longer intervals. For instance, it might be possible to shorten the overall laying period by producing eggs faster if eggs are smaller. However, there may be disadvantages in laying smaller eggs, as suggested by Ankney (1980), and a phenotypic trade-off between egg size and laying interval may be expected. But, long laying intervals may be prevented by time constraints, such as those imposed by an Arctic breeding season, for instance. Long intervals would

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likely lead to smaller clutch sizes given time constraints on the total laying period, and smaller clutches will in turn lead to fewer successful offspring (Rockwell et al. 1987). Therefore, we hypothesize that laying intervals are likely to be the result of evolutionary trade-offs between clutch size, time available for laying, and egg size. Studies of laying intervals of individual females would help to clarify whether such trade-offs are occurring.

In past studies, however, individual laying times and intervals have been largely ignored. While knowing general trends in laying behavior of a population is helpful (Bezzel 1962, Raveling 1978, Birkhead 1980, Lank et al. 1985, MacInnes and Dunn 1988), this knowledge alone cannot provide a complete understanding of events occurring during the egg-laying period and may lead to erroneous inferences about behavior of individuals. Studies that have addressed individual laying behavior are generally not well-controlled, utilizing incidentally collected data, nor do they make any attempt to consider confounding events or the effects of infrequent observations (Schubert and Cooke, unpubl. data).

In Lesser Snow Geese (*Chen c. caerulescens*), individual laying times and intervals have been inferred from population data. The laying period for a five-egg clutch is approximately six to seven days (Cooch 1958, Krechmar and Syroechkovsky 1978). Knowing this laying period, some hypotheses about laying interval in the Lesser Snow Goose can be eliminated (e.g., a constant laying interval shorter than 24 h or a constant 24-h interval). Others, however, cannot be eliminated so easily. The hypothesis of a variable laying interval is difficult to test without continuous observation, but preliminary observations indicate that laying interval is relatively constant (L. Gurtovaya, pers. comm., M. Bousfield, pers. comm.). The two hypotheses that we tested, therefore, are (1) Snow geese generally lay eggs at 25 h intervals, with the interval between some eggs, usually the fourth and fifth, being much longer (e.g., 45 h), such that eggs are always laid in the morning (Cooch 1958), and (2) Snow Geese lay with a constant interval longer than 24 h (e.g., 33.6 h, Krechmar and Syroechkovsky 1978). We also examine the effect of various factors (female age, egg size) that may influence laying interval and consider the effects of confounding events and infrequent observations on calculated laying intervals.

METHODS AND MATERIALS

Data were collected from 1980–1988 at the Lesser Snow Goose colony at La Pérouse Bay (LPB) (58°24'N, 94°24'W), approximately 40 km east of Churchill, Manitoba. Every year, a part of the colony was divided into small areas (approximately 1 km^2), each of which was assigned to a field assistant who carefully conducted daily nest searches. Nests were individually numbered and marked with stakes when found. Date and time of each nest visit were recorded. Nests were usually visited daily at approximately 24-h intervals. New eggs were numbered with a felt marker and weighed using a 300 g Pesola spring scale. If the parents were seen, their color phase and band numbers (if banded) were also recorded. This information allowed identification of individuals and provided information such as female age and body size from banding records. Only nests that were found at the one-egg stage, were observed daily, and were not predated before the onset of incubation were used for our analyses. The average amount of time (in h) elapsed between deposition of successive eggs was determined using the equation:

$$LI = (t_N - t_1)/(N - 1) \qquad (1)$$

where LI is the laying interval, t_1 is the time and date at which the first egg was found, t_N is the time and date at which the last egg of the clutch was found, and N is the clutch size.

Clutch size was defined as number of eggs found before onset of incubation (i.e., the eggs were consistently warm for at least three consecutive days). Nests in which two eggs were observed to have been laid on the same day (106 nests or 4% of the sample), nests with clutch sizes greater than six (seven or 0.26%), and nests at which an egg was found outside the nest cup (17 or 0.64%) were assumed to have been parasitized and were therefore omitted from the analyses (see Lank et al. 1989). Nests with two or more successive days on which no new eggs were found (24 or 0.90%) were also removed from the sample. Such nests were assumed to have been abandoned and subsequently taken over by another goose.

A second method to determine laying interval consisted of examining laying patterns. Laying pattern refers to the order and day of laying of the eggs. Each character represents the 24-h period between successive observations. Digits represent the egg-number of the new egg found, and are assigned in the order in which eggs are found. The "-" represents a day on which no new egg was found (NNEF).

Only nests of clutch size five were used because smaller clutches have too few laying patterns to distinguish between various hypothesized intervals, and larger clutches are less common and have a very high probability of containing the parasitic eggs (38–96%, Rockwell et al. 1987). Nests were included only if they were visited at 24 ± 1 h intervals. Otherwise, criteria for inclusion of nests were those used for method one. Expected laying patterns were calculated based on the assumption that if nests are observed at a constant interval of 24 h and eggs are laid at a constant interval, various patterns would emerge. For instance, a 24 h interval would result only in the pattern 12345, and a 48 h interval would result only in the pattern 1-2-3-4-5. A 36 h interval, however, would result in the pattern 1-23-45 in half of the nests and the pattern 12-34-5 in the other half, depending on time at which the first egg was found relative to when it was laid. Potential laying patterns were similarly calculated for all hourly intervals between 24 h and 48 h and the frequencies at which laying patterns were observed were compared to those expected under each interval.

In 1980, seven nests were visited twice daily, once in the morning and once in late afternoon. From these nests it is possible to determine more precisely the time interval during which eggs were laid.

Laying time of the first egg for 228 five egg clutches was also determined, assuming a 33 h laying interval. For each nest with an expected laying pattern, a time range during which the first egg could have been laid was calculated based on the time of its discovery. Each individual laying pattern could have resulted from the first egg being laid at some time within either a 3 h or 6 h period during the 24 h preceding its discovery. For instance, if the laying pattern was 1-234-5 and the first egg was found at 10:00 h CST, this egg must have been laid sometime between 01:00 h CST and 07:00 h CST. If the laying pattern was 12-34-5, however, the egg must have been laid between 22:00 h CST the previous day and 01:00 h CST that day. The midpoint of this time range was then calculated, assuming this was the time at which the egg was laid, and rounded to the nearest hour.

TABLE 1

AVERAGE NUMBER OF HOURS TO PRODUCE EACH EGG[a]

Clutch size	Sample size (number of clutches)	Hours per egg (± SD)
2	220	37.1 ± 16.4
3	431	36.4 ± 24.0
4	727	33.3 ± 9.4
5	362	32.7 ± 3.5
6	56	32.5 ± 5.4

[a] ANOVA: $F = 3.25$, $P = 0.001$, N = 1796.

RESULTS

The laying interval equation yielded intervals between 32.5 and 37.1 h per egg, assuming laying interval is constant (Table 1). The laying intervals in clutches of two or three eggs are significantly larger than those in clutches of four, five, or six eggs (ANOVA, $F = 3.25$, $P = 0.001$, N = 1796). A Tukey-Kramer test confirmed that the differences were indeed due to two and three egg clutches ($P < 0.05$).

Clutches in which an egg has been removed by a predator would have apparently fewer eggs and longer laying intervals, whereas clutches in which an egg has been added would have apparently more eggs and shorter laying intervals. These artifacts could lead to a negative correlation between observed clutch size and laying interval. Schubert (1990) showed parasitism to be unimportant, but predation could bias the measurement of the true laying interval in small clutches. Consequently, two and three egg clutches were removed from subsequent analyses. Since there is no significant difference between the laying intervals calculated for clutches of four to six eggs (ANOVA, $F = 0.82$, $P = 0.44$, N = 1145), these data were pooled.

A 33 h laying interval encompassed the greatest frequency of laying patterns observed in five egg clutches (75.6%, Table 2), a result consistent with Table 1. Observed and expected pattern frequencies at this interval did not differ significantly (Table 2; $\chi^2 = 4.52$, $0.10 > P > 0.05$, df = 4), though it could be argued that there is a marginal difference.

If some variation (±3 h) is assumed among birds, two laying patterns are added to those expected. In total, then, the patterns found in 92% of the nests are included (Table 2). Of the remaining nests, 5% have the pattern 12345, and 3% contained more NNEF's than expected (Table 2).

Thus, we assume that the laying interval is 33 ± 3 h and that most unexpected laying patterns are a result of variation among birds (as is suggested in Table 2). Unless otherwise stated, laying interval for all subsequent analyses was calculated using equation (1).

TABLE 2

OBSERVED AND EXPECTED FREQUENCIES OF LAYING PATTERNS

Laying pattern	Expected[a] frequency	Observed frequency	Observed number
123-45[b]	0.250	0.16	48
12-345[b]	0.250	0.18	54
12-34-5[b]	0.125	0.10	30
1-234-5[b]	0.250	0.23	70
1-23-45[b]	0.125	0.09	26
1234-5[c]	—	0.12	35
1-2345[c]	—	0.04	13
12345[d]	—	0.05	15
1-2-34-5[d]	—	0.003	1
1-23-4-5[d]	—	0.003	1
12-3-45[d]	—	0.006	2
1-2-345[d]	—	0.013	4
123-4-5[d]	—	0.006	2
Total		301	

[a] The expected frequency of occurrence of each laying pattern was calculated using the amount of time throughout the day during which the particular pattern could have occurred. That is, if a total period of six hours on the day of nest initiation could have resulted in a particular laying pattern, the expected frequency of that pattern was 6/24 or 0.25.

[b] Pattern expected under a 33 h hypothesis.

[c] Pattern not expected under 33 h, but expected under a 33 ± 3 h hypothesis.

[d] Pattern not expected under a 33 ± 3 h hypothesis.

Laying times can vary in two ways. First, it is possible that laying time of the first egg is fixed, with all birds beginning their clutches at roughly the same time of day, and subsequent laying times varying depending on laying interval. Alternatively, laying time of the first egg can vary randomly among individuals.

Number and proportion of first eggs laid during each hour of the day were calculated from laying patterns of five egg clutches, assuming a 33 h interval as determined by methods one and two (Fig. 1). Running means, calculated over 3 h and 6 h intervals, indicate that there is a significant peak in laying frequency from 07:00 h CST to 09:00 h CST ($\chi^2 = 27.5$, $P < 0.01$, df $= 7$). This peak, however, is small (incorporating less than 20% of the nests). Fig. 1 indicates that laying occurs throughout the day and night, with its frequency never deviating very far from that expected under a random distribution of laying times.

Nests visited twice daily indicated that four out of 25 eggs (all positions, five egg clutches) were laid between 10:00 h CST and 17:00 h CST (the "afternoon" period). This number may have been slightly higher because some nests were visited slightly later than 10:00 h CST or earlier than

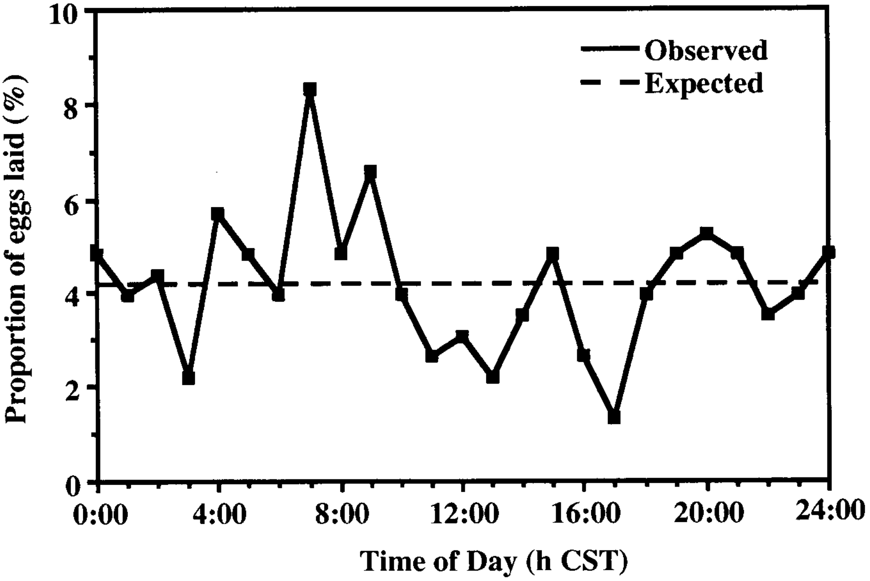

FIG. 1. Proportion of all first eggs laid at each time of day.

17:00 h CST. If laying is assumed to be random throughout the day, seven out of every 24 (or 7.25 out of 25) eggs should be laid during the "afternoon". There is no significant difference between the observed and expected laying frequencies for this period (Binomial test $P = 0.11$). The four "afternoon" eggs were laid by four different females, each of which usually laid during the longer interval, indicating that laying time does not merely vary among individuals but within individuals as well.

Laying intervals and laying times of the Lesser Snow Goose are presumably the result of natural selection, since they can affect the survival of young. Because they act through proximate processes, selection pressures can be better understood by examining the influence of environmental and physiological factors on laying times and intervals. We examined several such factors.

For physiological reasons (time required to deposit albumen or egg shell layers, or time required to convert nutrients into a usable form, for instance), females might be expected to lay smaller eggs more quickly than larger eggs, thereby shortening the overall laying period and gaining reproductive advantage by hatching their young earlier. We corrected for the positive correlation between egg size and female body size (Cooke, unpubl. data), as measured by tarsus length and body weight at banding (assuming this is an indicator of body size), by using egg size relative to

TABLE 3

AGE-SPECIFIC LAYING INTERVALS[a]

Age (yrs)	Sample size	Interval (h) ± SD
≤3	13	32.4 ± 6.2
4	23	34.5 ± 4.7
5	27	32.7 ± 2.3
6	24	32.6 ± 4.7
7	24	34.0 ± 3.9
8	27	31.6 ± 3.8
9	24	33.5 ± 4.4
10	18	32.4 ± 4.6
11	9	29.7 ± 5.0
12	12	33.5 ± 6.0
>13	8	30.7 ± 5.8

[a] ANOVA: $F = 1.39$, $P = 0.16$, N = 209.

female body size. Relative egg weight was not correlated with the laying interval in either case (tarsus: $R = 0.007$, $P = 0.28$, N = 179; mass: $R = 0.005$, $P = 0.32$, N = 195).

Females used to examine the effects of age in laying interval were between the ages of two and 16 years. Those over 12 years of age were grouped, as were those under four years. Laying interval at LPB was independent of female age (Table 3; ANOVA, $F = 1.39$, $P = 0.16$, N = 209).

Since factors such as egg size and hatchability vary within a clutch (Williams et al., in press), perhaps laying interval is variable also (i.e., eggs in certain positions within a clutch take longer to produce than others). The longer an egg takes to produce, the greater the probability of NNEF at that position within the clutch. In this study, NNEF frequency differed significantly depending on position within a clutch (Table 4; $G = 101.3$, $P < 0.001$, N = 4864), consistent with the differing frequencies at which certain laying patterns occur.

For each day during nest initiation each year, the proportion of active nests with NNEF was calculated. Only in two years, 1982 and 1985, were there significant differences between days in percentage of nests with NNEF (1982: $G = 20.75$, $P = 0.008$, N = 844; 1985: $G = 17.58$, $P = 0.014$, N = 439). Environment Canada weather data for Churchill, Manitoba, showed no adverse weather conditions on days of, or the days preceding, unusually high NNEF frequencies. That is, there was no snowfall and temperatures averaged above freezing. A principal components analysis to determine the contribution of temperature, total rainfall, and total

TABLE 4
PROBABILITY OF NNEF BEFORE CERTAIN EGG NUMBERS

Clutch size[a]	Egg number 2	3	4	5	6
2	0.46				
3	0.38	0.46			
4	0.36	0.29	0.46		
5	0.42	0.31	0.28	0.47	
6	0.46	0.27	0.33	0.31	0.38

[a] $G = 101.30$, $P < 0.001$, N = 4864.

snowfall to "weather" indicated no significant correlations between NNEF frequency and principal component 1 in any year of the study (Table 5). Apparently, immediate weather conditions have no detectable effect on laying interval.

If factors affecting laying interval covary from year to year, differences in calculated laying intervals between years could occur even though the effect of one factor alone was undetected. Laying interval was dependent on year (Table 6; ANOVA, $F = 6.52$, $P < 0.001$, N = 1140), although all intervals were well within three hours of 33 h. There is no significant correlation between either parasitism frequency and laying interval ($R = 0.105$, $P = 0.82$) or between predation frequency and laying interval ($R = 0.358$, $P = 0.36$) in any year.

DISCUSSION

A 33 h laying interval, obtained by using two methods, indicates that the phenomenon of not finding a new egg on a certain day in the laying sequence is likely an artifact of data collection methods rather than a bird's varying her laying interval. This is consistent with Krechmar and Syroechkovsky's (1978) hypothesis of a constant interval longer than 24 h. Y. Gurtovaya (pers. comm.) and M. Bousfield (pers. comm.) have recently observed a similar interval in Snow Geese nesting elsewhere.

The marginal difference found between observed and expected frequencies of laying patterns may be eliminated by addition of the two laying patterns produced by assuming a ±3 h variation among birds. Statistical analysis to determine the extent of laying interval variation would not be valid, however, because some patterns expected under various laying intervals can be the same. To predict frequencies with which each pattern should occur, assumptions must be made about what proportion of the population lays at each interval. Eventually, assumptions

TABLE 5

CORRELATIONS OF PROBABILITY OF NNEF WITH WEATHER[a]

Year	Pearson correlation coefficient	Probability
1980	0.260	0.50
1981	0.051	0.91
1982	−0.017	0.97
1983	0.450	0.31
1984	0.634	0.13
1985	−0.481	0.23
1986	0.760	0.14
1987	−0.373	0.54
1988	−0.027	0.95

[a] Principal component one of temperature, total rainfall, and total snow.

that fit the observed frequencies would be found, but their validity would remain uncertain. Therefore, we assume that there is variation among birds, but the mode is 33 h.

Those nests that are not consistent with a 33 ± 3 h laying interval may result from either undetected nest parasitism, or predation or from females with extreme variation around the average 33 h interval (e.g., 25–29 h for the pattern 12345 or >37 h for other patterns). A shorter than 33 h laying interval is more plausible for nests with laying pattern 12345, since parasitism frequency is too low to account for these. Nests with more NNEF's than expected could result from undetected predation or from a laying interval longer than 33 h. Continuous surveillance of nests is re-

TABLE 6

MEAN LAYING INTERVALS BY YEAR[a]

Year	Sample size (clutches)	Mean laying interval (± SD)
1980	148	33.4 ± 4.0
1981	162	32.9 ± 4.2
1982	217	33.7 ± 4.6
1983	94	31.4 ± 4.1
1984	111	32.1 ± 4.2
1985	107	34.0 ± 4.0
1986	87	32.2 ± 4.5
1988	160	32.9 ± 4.1

[a] As determined using method one; ANOVA: $F = 6.52$, $P < 0.001$, N = 1140.

quired to determine events leading to these anomalous observations and to determine the extent of variation in laying interval among geese in the colony.

Geese have traditionally been thought to lay their eggs in the morning hours. There is, however, evidence to suggest that laying occurs at other times of day as well (Cooper 1978, Johnsgard 1961, Kossack 1950, Owen 1980, Williams 1967, Young 1972). For the 33 ± 3 h laying interval to be correct, Snow Geese must vary laying times. Our analyses confirmed that laying of first eggs occurs at any time of day, and that females vary laying times, even within a single clutch.

Hypothetically, relatively large eggs take longer to produce. If an egg is very large relative to size of the female, extra time may be required to obtain necessary nutrients on the breeding grounds (Gauthier and Tardif 1991) or to convert them into a usable form if stored before arrival at the breeding ground (Ankney and MacInnes 1978). However, relative egg size of Lesser Snow Geese did not affect laying interval. Therefore, there is no evidence that geese reduce laying intervals through production of smaller eggs.

Young Snow Geese lay smaller eggs (Newell 1988) and smaller clutches later in the season (Finney and Cooke 1978, Hamann and Cooke 1987) than do older birds. Thus, young birds, especially first-time breeders, may also have a longer laying interval. M. Bousfield (pers. comm.) has observed an interval of 39 h in first-time breeders in a captive flock where the interval in experienced birds was approximately 36 h. In contrast, we found that laying interval did not change with female age. However, our sample of known first time breeders was small and may not accurately reflect behavior of this group. Further investigation is necessary to determine effect of age and experience on laying interval in geese.

Under Cooch's (1958) hypothesis, NNEF frequency should be very high before the fifth egg of a clutch, and close to zero before any other position. This was not true, however. Under a constant 33 h hypothesis, given random laying times for the first eggs, NNEF should be equally likely at all positions. However, because certain laying patterns have different expected frequencies than others, depending on the amount of variation around the 33 h laying interval, corresponding variation in NNEF frequency is expected among positions. Unfortunately, this hypothesis cannot be tested statistically because of the unquantified variation in laying interval. Nevertheless, our data suggest a 33 ± 3 h laying interval because the NNEF frequency is relatively high for all positions in all clutch sizes and does not peak before the fifth egg of five and six-egg clutches.

Weather may also influence a female's laying schedule. For instance, some passerines do not lay on extremely cold days (von Haartman 1951). However, a delay due to weather may be disadvantageous in an Arctic breeding season, because this would lengthen the laying period. Under the time constraints of the Arctic breeding season, an entire brood can be lost due to a delay of a day or two. Indeed, delays in egg deposition due to severe weather do not seem to occur in the Lesser Snow Goose.

Although significant differences in laying interval were found between years, these differences were small (all within 33 ± 2 h) and may be due to sampling a different group of females each year. However, further analyses of variables such as snow cover, food availability, number of nest sites available, and predator density, are needed to determine whether yearly variation is the result of variation in environmental factors.

For our analyses, we assumed that nests were found within 24 h of the first egg being laid, as nesting areas were checked very carefully each day. If nests were missed on the first day, frequency of nests with NNEF after the first egg, as well as laying period for the clutch, were underestimated. The probability that a nest was not found on its first day is very low, however. Also, the effects of such nests on calculated laying intervals would be strongest in the smaller clutch sizes. Because these were removed from most analyses, detectable effects of a small number of such nests were also removed.

Further research is necessary to answer questions raised in our study. Ideally, to eliminate many uncertainties, nests should be observed 24 h per day to determine individual behaviors. However, factors such as disturbance of the bird, location and type of nest, and inability to see nests clearly at a distance often make such observations impractical. Because data collection methods are often limited by available resources, alternative methods of answering pertinent questions must be found. For instance, more frequent observations can provide a more precise estimate of laying interval. Alternatively, laying patterns can be used. Although these methods still leave room for uncertainty, they provide better estimates of individual laying times and intervals than previous studies. This study makes use of such methods as well as considering the effects of confounding events.

We document the length of the laying interval of the Lesser Snow Goose and examine, in detail, some factors that may affect this interval. However, to understand fully the evolutionary implications of laying intervals, equally detailed data are required not only for other populations of Lesser Snow Geese, but for other species of waterfowl and for wild birds in general. When such information becomes available, it may lend further insight into the evolutionary processes that have shaped laying times and intervals in birds.

ACKNOWLEDGMENTS

We thank the staff and students at the Queen's Univ. Tundra Biology Station, La Pérouse Bay, Manitoba for their data collection efforts. We also thank Yena Gurtovaya and Marjorie Bousfield for information regarding laying intervals in other colonies of Snow Geese, and two anonymous reviewers for their comments on earlier versions of the manuscript.

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