

## REPRODUCTIVE HABITS IN THE SNOW GOOSE: THE INFLUENCE OF FEMALE AGE

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Parental age influences reproductive performance in several avian species. Clutch size increases and nesting becomes earlier after the first year of breeding in certain species (e.g., Great Tit (*Parus major*), Kluijver 1951; Black-legged Kittiwake (*Rissa tridactyla*), Coulson 1966; Canada Goose (*Branta canadensis maxima*), Brakhage 1965). Other species show no effect of female age and, in a few instances, clutch size declines with age (see Klomp 1970). The correlation of parental age with hatching and fledging success shows similar variability among species.

In many colonial nesting species, young birds establish territories in peripheral or marginal habitats (e.g. Coulson 1971) either because of their inferior competitive ability in acquisition of central nest sites (Cooch 1958, Wynne-Edwards 1962) or because adults, nesting earlier, establish central territories by precedence (Coulson 1971).

The Lesser Snow Goose (*Anser caerulescens caerulescens*; Delacour 1954) has been under study at a small nesting colony (3,000 pairs) at La Pérouse Bay, Manitoba (58°24'N 94°24'W) since 1968. Many of the birds of this colony are individually identifiable through coded plastic leg bands. In this paper, we examine the age of females as a factor affecting the spatial distribution of nests in the colony, reproductive success and the timing of nesting. Annual differences in the proportion of young birds that nest are also examined.

Male geese that hatch at La Pérouse Bay seldom return to the colony after reaching reproductive maturity (Cooke et al. 1975). We have, therefore, been unable to establish a population of banded males of known age and to examine the influence of male age on reproduction.

### STUDY AREA AND GENERAL BIOLOGY

The nesting colony is located along the west side of La Pérouse Bay in the Mast River Delta. The river is shallow, seldom exceeding 0.5 m, and the adjoining mainland and many islands are barely above water level at their highest points. The vegetation shows a successional trend from the coastal mud-flats to in-

land areas. The dominant species in each vegetational zone are: (1) salt marsh (*Puccinellia* spp., *Carex salina*), (2) short grasses (*Festuca* spp., *Calamagrostis neglecta*), (3) tall grasses (*Elymus arenarius*), and (4) scrub willows (*Salix* spp.).

The arrival of geese in mid-May usually coincides with the onset of spring melt. The amount of snow cover, ice conditions and water level at this time vary greatly between years. The geese are mated when they arrive; nesting territories are established as soon as bare ground appears. Thus, the condition of the habitat is an important variable in determining the phenology of nest initiation and the ultimate number of breeding pairs (Cooch 1961, Barry 1962, Finney 1975).

The nest history information reported here was collected in 1973 and 1974. In 1973, the geese arrived after much of the nesting area was exposed and dry. We first found a nest on May 24 and nest initiation continued until June 4. In 1974, the nesting area was snow-bound when the geese arrived but a rapid melt ensued and nesting sites quickly became available. Although the birds apparently delayed nesting by a few days, snow and water conditions did not obviously restrict the number of nesting pairs. Nest initiation began on May 27 and continued until June 9.

Snow and water first leave areas where vegetation is low. Locally, higher ground is first available for nesting. Areas which are colonized first are ultimately those of highest nesting density. Usually one egg is laid per day until the clutch is complete (Cooch 1958, 1961). Intraspecific nest parasitism (i.e. females laying eggs in nests other than their own) is a frequent phenomenon although it varies between years (5-11% of successful eggs, unpubl. data). Incubation commences after the laying of the last or penultimate egg and averages 23.7 days (SD = 1.06, N = 250, unpubl. data). Within a day of hatching, the goslings leave the nest site with their parents. The families form loose flocks and feed mainly on the newly emergent vegetation (Lief 1973). During this period the adults molt their primaries. Their reacquisition of flight capability corresponds closely to the fledging of goslings at seven weeks of age (Cooch 1958). The geese begin their long southward migration in late August and early September.

Maturity is deferred in both sexes and birds cannot breed until two years old (Cooch 1958). Not all birds first breed at this age; some wait until at least four years of age.

### METHODS

Prior to the arrival of the geese in each year, we delineated an area of the colony as the primary study area. This area was searched daily during nest initiation and information was collected on each nest as the geese established territories. Peripheral areas

TABLE 1. Number of females marked as goslings in 1970–1972 and observed at La Pérouse Bay 1972–1974.

		Year banded						
		1970		1971		1972		
Number banded		1405		442		1181		
Year resighted	N	$\tau$	N	$\tau$	N	$\tau$	Total examined (e)	
1972	13	0.9**		—		—	1064	
1973	53	2.8**	36	6.2		—	1332	
1974	73	4.0**	33	5.9	44	2.9**	1280	

		Year banded						
		1970		1971		1972		
Year recaptured	N	$\tau$	N	$\tau$	N	$\tau$	Total captured (e)	
1972	26	2.5**					736	
1973	65	5.9**	24	6.9			786	
1974	63	7.4**	17	6.3	42	5.9**	607	

\*\* Significant difference ( $P < 0.01$ ) between return rate estimates by resight and those obtained by recapture ( $2 \times 2$  contingency tables).

were included in the study area in 1974. The study areas contained 514 nests in 1973 and 730 in 1974.

The starting date of a nest was considered precise if there was only one egg in the nest on the date of nest discovery. Eggs were marked when discovered and their subsequent fate monitored. Total clutch size was recorded as total number of eggs seen in a nest.

During incubation, nests were visited every 3–4 days and nest destruction or egg loss was noted. As incubation proceeded the pairs became less sensitive to our disturbance and it became possible to identify the resident of a particular territory. At this time, parental color phase and the bands on each bird were recorded.

Except where otherwise indicated, "adults" refers to birds at least four years old, i.e. banded as adult-plumaged birds two or more years previously. The inclusion of some four-year-old birds in the adult category renders comparison of adults and four-year-olds less sensitive, but this penalty was accepted in order to assure an adequate sample of adult birds.

During incubation a secondary study area was established containing 1087 nests in 1973 and 1372 nests in 1974. The data collected in this area did not include initiation or start of incubation dates but in other respects were identical to those in the primary study area. In selecting our study areas we attempted to obtain a sample of nests that was representative of and proportional to the various habitat types and nesting densities on the colony. The location of each nest was mapped using aerial photographic prints (National Air Photo Library, negative numbers A17166-62, -39:  $\times 10$ , scale 1:1200). The resolution and scale of the photos allowed mapping of the nests to an accuracy of 3 m.

When hatching began, nests were again visited daily. The date of hatch was defined as the first day that any egg in a nest was observed pipping. Only

successful nests (at least one egg hatched) for which a precise hatch date was known were included in our analysis. The hatch date was considered imprecise if there was no record for the nest on the day immediately preceding the first observation of goslings or pipping eggs in a nest. At this time the pair's productivity was recorded as the number of goslings leaving the nest (number of eggs hatched, or presumed hatched, minus the number of goslings seen abandoned). For future identification, goslings were individually marked with metal tags applied to the web.

Approximately five weeks after hatching, flocks of flightless adults and young were captured. Bands were applied to each unbanded bird, which color coded them as to year when first banded and their age. Previously banded birds were noted and this provided the basis for one estimate of return rate. All young of the year were examined for web tags.

Computer analyses of the data were done with the APL language, using its FILE system capabilities. Statistics follow Sokal and Rohlf (1969).

## RESULTS

### RETURN RATE

The return of birds marked as goslings to the breeding colony in their second and subsequent years is recorded in Table 1. The return rate has been estimated from data obtained by (a) examining females for leg bands during incubation (resight), and (b) recapture of banded birds four to six weeks later. The data have been normalized and are presented as values that give a relative measure of the proportion of the population which is of a

specified age group. The values were calculated using the equation

$$\tau = n_{ij} / (b_i e_j) \times 10^5$$

where,  $n_{ij}$  = number of class relocated in year  $j$  from banding year  $i$ ;  $b_i$  = number of class banded in year  $i$  (♀ only);  $e_j$  = number of females examined in year  $j$ . Multiplication by  $10^5$  is arbitrarily introduced to make the table more readable.

Due to simple dilution, the  $\tau$  values decrease as the population increases. For the purpose of these analyses, we therefore make the simplifying assumption that the nesting population was constant between 1972 and 1974. Actual estimates of the colony size by Sulzbach (1975) over this period range between 2,950 and 3,450 pairs but the confidence intervals of these estimates overlap. Thus, the assumption of constant population size is reasonable.

Comparing corresponding entries in Table 1a and 1b, estimates of return rate from recaptures consistently exceed those obtained from resighting. These differences are highly significant ( $P < 0.01$ ) for females banded in 1970 and 1972, but not for those banded in 1971. These differences apply to all recovery years examined.

This discrepancy in estimates of return rate (as calculated from the recapture versus the resight data) indicates that errors or sampling biases have been introduced to one or both of the data bases. The discrepancies apply constraints on the interpretation of the return rate data. However, differences in return rates are assumed to be real when they are large and when the two methods show a consistent pattern.

Comparison of entries along the major diagonals of Table 1a and 1b shows that a much larger proportion of 1971 goslings returned as 2-year-olds than did those hatched in 1970. Females that hatched in 1972 were intermediate. Important differences also exist in the pattern of return for each year-class as 2-, 3-, and 4-year-olds. Females of the 1970 year-class returned in gradually increasing proportions with increasing age. However, females of the 1971 year-class showed a marginal decline in proportionate return between 2 and 3 years of age.

Sulzbach (1975: Table 20) using different techniques found a similar variation in the proportion of nesting 2-year-olds. He estimated that 12%, 47% and 52% (1970, 1971 and 1972 year-classes, respectively) of those females which were still alive nested as 2-year-olds. The estimates depended solely on re-

capture data which also provided the basis of the annual mortality calculations.

Sulzbach's (1975) calculations show that the year-class variation in 2-year-old return cannot be adequately explained by assuming that it reflects differential mortality among the cohorts. Band recoveries indicate that goslings in 1971 may have suffered lower mortality due to hunting than did the goslings of 1970 and 1972 (7.9% vs. 10.2% and 10.1% direct recoveries; Sulzbach 1975: Table 8). This discrepancy is, however, insufficient to explain the large variation in return rates which has been described.

The variation in observed rates of return can best be explained by assuming that it reflects differences in recruitment rates of young birds to the nesting population. The resight estimates rely, of course, on data obtained from nesting birds. The birds which are recaptured during the banding program are also predominantly nesting birds and their young because most non-nesting adults leave the area of the colony prior to the banding program (Boag 1974, Sulzbach 1975).

The different return rates may be due to differences between years in the intensity of competition for nest sites and/or differences in the competitive ability of the specific year-classes. At present, we have insufficient information to distinguish between these alternatives.

Regardless of the reasons for differential return rates among year-classes, one consequence of this is important. Many females born in 1971 were experienced nesters as 3-year-olds whereas a large proportion of 1970 females were inexperienced nesters at this age.

#### SPATIAL DISTRIBUTION

The spatial distribution of nests was analyzed to determine how nest sites were distributed with respect to female age. A preliminary analysis in which the number of 2-year-olds, 3-year-olds and adults was compared among study areas showed that in each year the age-classes were distributed non-randomly (1973:  $\chi_6^2 = 40.6$ ,  $P < 0.001$ ) (1974:  $\chi_6^2 = 29.9$ ,  $P < 0.001$ ).

The resolution of age-class distribution was improved by dividing the colony into rectangular blocks of approximately 4 ha. The information obtained was used to generate the isograms in Figure 1. This represents the distribution in 1973, which differs in detail from 1974, but maintains the general pattern.

A similar map indicating the density of nesting birds on the colony in 1973 was generated

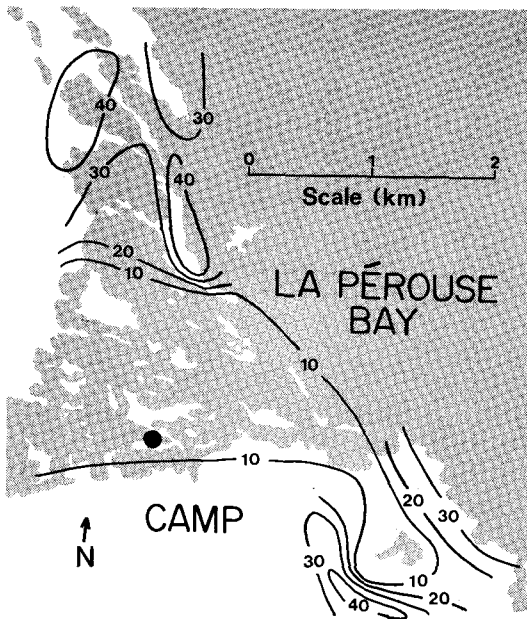


FIGURE 1. Isograms indicating percent of marked females two or three years of age.

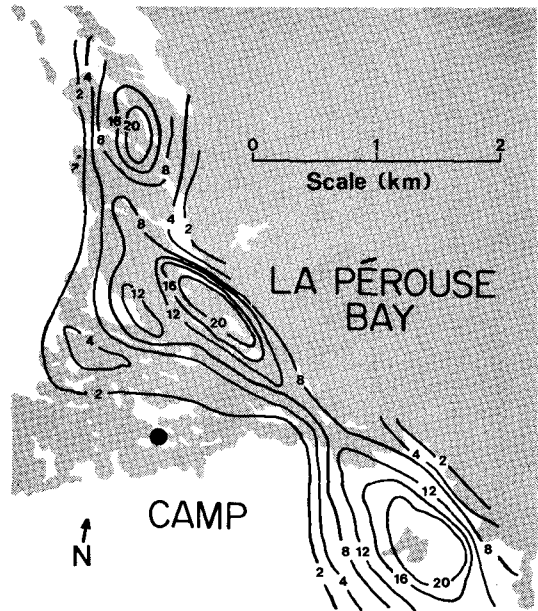


FIGURE 2. Isograms indicating nests per hectare of land.

to test the hypothesis that young birds nest predominantly in low density areas (Fig. 2). In the calculations of area, water bodies were excluded and the density figures represent nests per unit of land area. No consideration was given to other variations in habitat suitability among areas because these data are not readily available. Both successful and unsuccessful nests have been included in making the density isograms because density during nest initiation was considered the relevant parameter as an indicator of intensity of competition and nest site availability. The nest density pattern was similar in 1974.

Comparison of the two figures shows that most adult birds were found in areas of high nest density and younger birds in low density and peripheral regions. The central delta region, however, was an exception, because the nests there were of low density but there were very few young female birds. Nesting density as calculated, therefore, presents an incomplete explanation of the age-dependent spatial distribution of birds on the colony.

Coulson (1971) defined the most recently utilized portion of a colony as "peripheral," and he found that young Black-legged Kittiwakes occupied these areas. If one additionally defines a peripheral site as one that is only irregularly available for nesting, then the spatial distribution of Snow Geese of different ages is adequately explained. Much of the central delta has been consistently occupied since the study began in 1968 and now

has a high percentage of adult birds. The northern part of the study area was not colonized until 1972 and more than 30% of the banded birds in this area are 2- or 3-year-olds. It is not known when the outer regions in the south were first colonized (pre-1969) but a striking feature of the area is that young birds were in fringe areas that had been occupied in only four of five breeding seasons since 1970.

Thus, young breeding females were clustered on the colony in sites that can be defined as "peripheral" according to three criteria: (a) nesting density, (b) recency of colonization and (c) constancy of nest site availability between years.

#### TIME OF NESTING

Parameters of nesting timing were compared among the age-classes. Comparative nest initiation dates for 1974 are presented in Table 2. Both adult and 4-year-old females estab-

TABLE 2. Effect of female age on mean date of nest initiation as affected by female age 1974 (dated from May 1).

Age	$\bar{x}$	SD	N
2 years	33.6	1.77	8
3 years	33.0	1.73	3
4 years	29.7	1.41	9
Adult ( $\geq 4$ )	30.5	1.92	35

t-test shows that 2- and 3-year-old birds start their nests significantly later than 4-year-old and adult birds ( $P < 0.01$ ).

TABLE 3. Effect of female age on mean hatch date, 1973 and 1974 (June).

Age	1973			1974		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N
2 years	26.7	2.33	32	28.2	2.10	19
3 years	25.2	2.21	52	26.7	1.59	26
4 years	24.7	2.39	12	26.3	1.59	53
Adult ( $\geq 4$ )	24.1	1.77	179	26.3	1.86	177

In 1973, t-tests show that mean hatch dates of 2-year-olds were significantly different from those of 3-year-olds, which in turn were significantly different from those of adults ( $P < 0.05$ ). The differences between 2-year-olds and adults are highly significant ( $P < 0.01$ ). In 1974, 3-year-old, 4-year-old and adult birds did not differ significantly from one another. Two-year-olds were however significantly later than the combined older birds ( $P < 0.05$ ).

lished nests three days earlier than did either 2- or 3-year-olds. Similar data were not available for 1973 as most 2- and 3-year-old females nested outside of the primary study area.

Hatch dates can be used as an alternative measure of timing. The duration of incubation does not vary significantly with female age (unpubl. data) and hatch date can thus be used to indicate the date of nest initiation. Some resolution is lost, however, because early nests have larger clutches and incubation does not commence until the last or penultimate egg is laid. Thus, the starting date of large clutches is earlier relative to hatch dates than is usually the case for smaller clutches.

The mean hatch dates are presented for the various age-classes of both 1973 and 1974 in Table 3. The pattern of differences varied between the two years in one respect. Three-year-olds hatched later than adults in 1973 but not in 1974. If one assumes that timing may be affected by experience as well as physiological age as such, then one would anticipate this result because in 1974 a larger proportion of 3-year-olds had bred as 2-year-olds, than in 1973.

#### TOTAL CLUTCH SIZE

The mean total clutch size for females of different ages is compared in Table 4. In 1973, adults averaged more eggs than 3-year-olds who in turn had a larger average clutch than 2-year-olds. The sample of 4-year-olds was too small for statistical comparison. In 1974 the average clutch size of 2-year-old females

was smaller than that of all other age-classes. The average clutch of 3-year-olds, however, did not differ significantly from that of 4-year-olds nor from that of adults while that of 4-year-olds was significantly smaller than that of adults.

These results are again consistent with the hypothesis that experience itself can affect clutch size since most 3-year-olds in 1973 were inexperienced birds, while a larger proportion of those of 1974 had bred as 2-year-olds in the previous season. The smaller average clutch of 4-year-olds relative to adults may reflect the fact that in 1974 there was still a significant proportion of first-time breeders among this 1970 year-class.

Clutch size is known to be negatively correlated with time of nesting in Snow Geese (Cooch 1958). Lemieux (1959) postulated that this correlation was due to the fact that inexperienced females nested later and had smaller clutches thus depressing the mean as the season progressed. As he was studying an unmarked population, his hypothesis was untested.

Using initiation dates, sample sizes were inadequate in 1973 but data were available for 1974. There was a significant negative relationship between initiation date and total clutch size for amalgamated age classes ( $b = -0.34$ ,  $F_{1,88} = 37.34$ ,  $P < 0.01$ ). There was no significant correlation found within 2-, 3- or 4-year-old classes, but samples were small (7, 2 and 8 respectively).

When hatch date was used as the parameter

TABLE 4. Mean total clutch size as affected by female age: 1973 and 1974.

Age	1973			1974		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N
2 years	3.06	1.07	36	3.69	0.869	42
3 years	3.87	1.19	53	4.59	1.500	32
4 years	4.46	0.78	13	4.43	1.330	72
Adults ( $\geq 4$ )	4.68	1.01	183	4.87	1.393	233

In 1973, t-tests show that 2-year-olds had significantly smaller clutches than 3-year-olds, which were significantly lower than adults ( $P < 0.05$ ). The differences between 2-year-olds and adults are highly significant ( $P < 0.01$ ). In 1974, t-tests show highly significant differences between 2- and 3-year-olds, between 2- and 4-year-olds, and between 2-year-olds and adults ( $P < 0.01$ ). The difference between 4-year-olds and adults is significant at the 0.05 level.

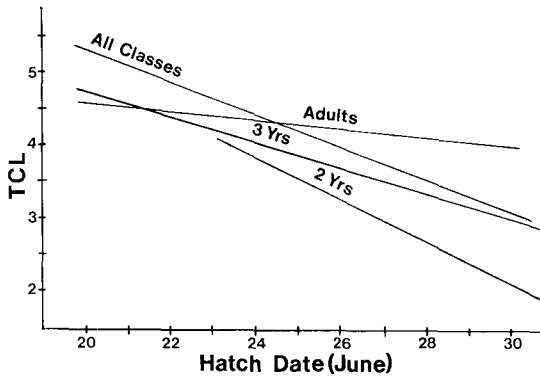


FIGURE 3. Total clutch size (TCL) vs. hatch date for nests of known-aged females (1973 data: best linear least-squares approximation).

b = Slope, r = Correlation coefficient, P = probability

	b	r	P
All classes	-0.20	-0.37	<0.01
Adults	-0.09	-0.16	<0.05
3-yr-olds	-0.14	-0.25	n.s.
2-yr-olds	-0.27	-0.61	<0.01

of timing, the negative relationship disappeared in the 1974 data. This reflects the fact that females who started early had, on average, larger clutches and took longer to start incubating.

The relation between hatch date and clutch size in 1973 is presented in Figure 3 in linear least-squares format for all female age-classes studied. Except for 3-year-olds and for the pooled data, the negative regression is significant ( $P < 0.05$ ). The lack of correlation for the 3-year-old class may reflect a small sample size ( $0.10 > P > 0.05$ ). The reasons for the presence of a significant relationship between hatch date and clutch size in 1973 and its absence in 1974 is not clear.

We conclude that the observed negative regression between clutch size and time of nesting was not simply an artifact of the age structure of the population, because the relation

held within specific age-classes. As younger females tended to start later and have smaller clutches than adults, it is not surprising that the negative slope of the regression is reduced when comparing the adult class to the amalgamated sample. The difference in slope, however, is not significant.

The 1973 data can be further used to test the hypothesis that young females have smaller clutches simply because they nest later. Average clutch sizes on a given hatch date were compared among age-classes and the results are presented in Table 5. For four of the five dates for which a comparison of adult and 2-year-olds was possible, the difference in average clutch size was significant. A similar comparison of 3-year-olds and adults yielded significant differences in clutch size on four of eight days. No differences were found when 2-year-olds and 3-year-olds were compared. These results lead to the conclusion that the differences in average clutch size among age-classes are not adequately explained by differences in the time of nesting.

#### NESTING AREA EFFECTS

As adults and young birds nested in different areas of the colony, it was necessary to determine if the smaller clutches and later timing of young birds was a consequence of their choice of nest sites. Adult and 2-year-olds were selected for comparison from areas of young female concentration and from areas of adult concentration (>40% and <10% of marked females were 2- or 3-year-olds, respectively). Throughout this section these areas are referred to as "young-frequent" and "young-infrequent" areas, respectively. A sample of 2-year-olds and adults was selected from each area. Hatch dates and clutch sizes were compared within areas between age-classes and for the same age-class between areas. Few 2-year-olds were discovered in the young-

TABLE 5. Paired comparisons of average clutch sizes among age-classes on specified hatch dates, 1973.

Hatch date	2 yr. vs. Adult			2 yr. vs. 3 yr.			3 yr. vs. Adult		
	t	d.f.	P	t	d.f.	P	t	d.f.	P
June 21							0	4	1.0
June 22							0	24	1.0
June 23							-0.21	34	0.418
June 24	-0.94	52	0.825	1.37	11	0.099	1.89	59	0.032*
June 25	2.73	31	0.005**	1.01	11	0.167	1.98	38	0.28 *
June 26	3.35	21	0.001**	-0.77	10	0.230	2.20	23	0.019*
June 27	5.27	19	0.001**	-1.46	16	0.082	2.47	18	0.012*
June 28	2.40	6	0.027*						
June 29							0.15	4	0.444

\* Difference is significant ( $P \leq 0.05$ ).

\*\* Difference is highly significant ( $P \leq 0.01$ ).

TABLE 6. Hatch dates of broods by the age of female parent and the nesting area (dated from June 1). >40%—for nesting area corresponds to areas where >40% of the marked females were 2 or 3 years old. <10%—refers to areas with <10% of these age-classes.

(a) 1973					
		Mean	S <sup>2</sup>	N	
>40%	{	adults	24.1	2.47	20
		2 yr.	26.5	4.73	14
<10%	{	adults	23.2	1.25	19

(b) 1974					
		Mean	S <sup>2</sup>	N	
>40%	{	adults	26.7	1.44	30
		2 yr.	28.2	4.97	6
<10%	{	adults	26.6	4.36	84
		2 yr.	29.0	5.00	7

In 1973, in the >40% area, adults had a significantly earlier hatch date than 2-year-olds ( $P < 0.05$ ). Adults in the <10% area had a significantly earlier hatch date than adults in the >40% area. In 1974 in the <10% area, adults hatched significantly earlier than 2-year-olds ( $P < 0.01$ ); other differences were not significant.

infrequent area in 1973, and comparisons involving these birds are thus missing.

Comparison of mean hatch dates (Table 6) reveals that the mean date of clutches of 2-year-old females was later than that of adults nesting in the same area. The difference is highly significant except in the 1974 young-frequent area, where significance was lacking. In this area, 2-year-olds were on average 1.5 days later than adults.

When adults and 2-year-olds were compared, differences in hatch date between the two areas in 1974 were not significant. However, adults in the young-infrequent area did hatch their clutches significantly earlier than those in the young-frequent area in 1973. Comparisons of timing of an age-class between areas are sensitive to factors such as relative snow cover and water level at initiation. As these factors vary widely between nesting seasons, the apparent inconsistency in results is not surprising.

Comparing mean clutch sizes (Table 7) shows that, within an area, 2-year-olds had a smaller average clutch than did adults. The differences are significant except in the 1974 area of young concentration, where the difference was only 0.47. No significant differences in average clutch size were found for an age-class between areas.

In summary, differences between adult and 2-year-old females, in both time of nesting and clutch size, were not a consequence of the location of their nests.

TABLE 7. Clutch size as affected by female age and nest location.

(a) 1973					
	Percent 2- and 3-year females		Mean	S <sup>2</sup>	N
>40%	{	2 years	3.33	0.81	15
		adults	4.65	1.61	20
<10%	{	adults	5.05	0.89	20

(b) 1974					
			Mean	S <sup>2</sup>	N
>40%	{	2 years	3.67	1.09	15
		adults	4.14	0.87	36
<10%	{	2 years	3.40	0.71	10
		adults	4.48	1.37	67

In 1973, 2-year-olds in the >40% area had significantly smaller clutches than adults ( $P < 0.01$ ). In 1974, 2-year-olds in the <10% area had significantly smaller clutches than adults ( $P < 0.01$ ). Other differences were not significant.

#### GOSLINGS LEAVING THE NEST

The relative productivity of the different age-classes did not substantially change in either year when the number of goslings leaving the nest was examined rather than clutch size (Table 8). Percentage egg success for successful nests was calculated for each age-class by comparing the mean number of goslings leaving the nest to the mean clutch size (Table 9). These data indicate that in successful nests, differences in egg success are slight among the age-classes. Information on relative nest success of the various age-classes was incomplete and therefore the small number of unsuccessful nests for which the age of the female parent was known (4 in 1973, 13 in 1974) were excluded from these analyses.

#### DISCUSSION

Clutches become larger and the time of nesting advances with female age in the Snow Goose as in several other avian species. Pevett (1973) previously noted that 2-year-old Snow Geese had a smaller clutch than adults. Although age-classes were heterogeneously distributed throughout the colony, neither hatch date nor clutch size differences were a direct consequence of differences in areas of nesting. Within any section of the colony there were, in differing proportions, both adult and young residents and in each, adults on the average started earlier and had larger clutches. Although clutch size was negatively correlated with time of nesting, the lower clutch size of young females was not simply a result of their timing, as those starting on the same dates as adults had a smaller average clutch.

TABLE 8. Mean number of goslings leaving the nest as affected by female age: 1973 and 1974.

Age	1973	SD	N	1974	SD	N
2 years	2.50	1.382	36	3.16	1.16	31
3 years	3.40	1.323	53	4.04	1.73	28
4 years	3.75	1.058	13	3.87	1.44	69
Adult	4.26	1.062	183	4.11	1.57	218

In 1973, significantly fewer goslings of 2-year-olds left the nest than those of 3-year-olds; significantly fewer goslings of 3-year-olds left the nest than those of adults ( $P < 0.05$ ). The difference between 2-year-olds and adults was highly significant ( $P < 0.01$ ). In 1974, 2-year-olds differed significantly from the other three classes combined ( $P < 0.05$ ).

Return rates of females of known age were estimated from observations of banded birds during incubation and from recapture of banded birds during the adult molt. Recapture estimates were consistently higher than those obtained from incubation data. One or both samples were apparently not random with respect to the La Pérouse Bay population. Randomness is an implicit assumption of the calculations.

One source of potential bias is in the proportion of recaptured birds which have successfully nested. The birds observed during incubation were mainly successful nesters. The recapture sample could possibly include a higher proportion of failed nesters and non-breeders, although evidence suggests that most of these birds are not captured during banding drives (Boag 1974, Sulzbach 1975). There is a considerable discrepancy among year-classes in the amount of difference in the two estimates of return rate. The 1970 year-class estimates are much more disparate than those of the 1971 birds. If differences in the proportion of successful nesting birds account for a large proportion of discrepancy in the two estimates of return rate, the data imply that the 1971 year-class was more successful than the 1970 year-class in both 1973 and 1974. The possibility of persistent year-class differences is speculative at present, but represents a potentially interesting phenomenon.

One further factor may be causing differences in the return rate estimates. Nesting females tend to associate with other birds of the same age. Similar segregation occurs in post-hatch feeding flocks (Finney 1975). Discrepancies in estimates of return rate could be explained if we were consistently monitoring

nests in areas that had a disproportionate number of adults and/or capturing post-hatch flocks biased towards younger females. If this were true, one would also anticipate that estimates of adult return rate would be substantially higher at nesting than at banding. Although the estimates of adult return rate at nesting are marginally larger in both years (1973:  $\tau = 18.2$  nesting vs.  $\tau = 16.3$  recapture; and 1974:  $\tau = 15.3$  nesting vs.  $\tau = 14.2$  recapture), the magnitude of the discrepancy does not approach that described for young females. These data suggest that our samples were large enough to overcome distributional biases. Unfortunately, the reasons for the discrepancy in return rate estimates remain unclear.

Apparently most female goslings hatched in 1971 bred in their second year while a relatively small proportion of 1970 goslings did so. After comparing the relative performance of these cohorts in their third year, we conclude that both breeding experience and chronological age are important in the determination of clutch size and timing (cf. Coulson 1966). We were unable to determine if first-time breeders of different age differed in these parameters as was discovered in the White Stork (*Ciconia ciconia*; Hornberger in Lack 1966).

In each year, several 2-year-old, and therefore inexperienced, females nested in predominantly adult areas and early relative to other females of the same age. These may represent those cases when a female acquired an experienced male and was thereby stimulated to nest earlier in the season (Coulson 1966, Mills 1973). Unfortunately, in no instance was the age of the male known; hence, the importance of the male in determining time and place of nesting remains entirely speculative.

In discussing the differences in clutch size among the age-classes we assume that the observed clutch size is an unbiased estimate of the real clutch size. Factors such as intra-specific nest parasitism (see Cooke & Mirsky 1972) which increases apparent clutch size,

TABLE 9. Percentage egg success of successful nests as influenced by female age.

Year	Age			
	2	3	4	Adult
1973	87%	89%	—	92%
1974	86%	87%	87%	89%



and replacement clutches (see Ryder 1971), which in a determinate layer result in a reduced clutch size, are assumed to be random events among the age-classes. We have no evidence, but both events are relatively infrequent.

Cooch (1958) first described the negative correlation between clutch size and timing in Snow Geese. Intraspecific nest parasitism and replacement clutches provide, if they are non-randomly distributed among the age-classes, for a biologically trivial explanation for this phenomenon. Other explanations fall into two categories: (a) proximate mechanisms governing clutch size and timing, and (b) ultimate factors responding to selective pressures.

A decline in hormone level after the population reproductive peak or changes in photoperiod or temperature response have been suggested as proximate factors causing the seasonal trend in clutch size among anatids (Johnsgard 1974). The efficiency of a female in acquiring adequate resources for egg laying has been postulated to affect both clutch size and timing (Perrins 1965, Lack 1966); thus late nesters may simply represent the inefficient members of the population.

Alternatively, females starting later may render the hatch of their young more synchronous with early nesters by laying fewer eggs, thereby starting incubation sooner. This may be advantageous if habitat conditions such as food supply are optimal near the hatch date of early nesters (Lack 1954), or if, through synchronization, the probability of gosling predation is significantly reduced (Barry 1962, Patterson 1965, Nisbet 1975).

With present information, it is impossible to determine the relative merits of these possible explanations. It is first important to determine if real clutch size, as opposed to observed clutch size, declines with the season. If this is established, then one can reasonably proceed to identify the proximate mechanisms involved and the selective factors which led to the development of these mechanisms within the context of the reproductive habits of the species.

Aside from nesting later and having smaller clutches, young females were found to nest predominantly in peripheral areas of the colony. Whether young birds prefer peripheral areas or are excluded from more central regions because of social interactions (Wynne-Edwards 1962), or because adults, nesting earlier, simply exclude young birds by precedence (Coulson 1971), is not known.

Older birds may return to the same areas of the colony each year because of habitat

selection and/or site tenacity. Our observations confirm Cooch's (1958) conclusion that site tenacity is present but weak in Snow Geese. Of 34 pairs of successfully nesting geese found in both 1973 and 1974, only 15 were in the same neighborhood (within 50 m) and 50% of the pairs had moved territories more than 70 m between seasons. Thus nest site tenacity is not well enough established in the species to ensure that a group of birds will nest in the same area each year and some type of habitat selection therefore appears to be in effect. This selection may be based on temporal patterns of nest site availability rather than physical characteristics of the areas. The nature of the selection is obscure, but our data show that mechanisms such as site or neighborhood tenacity are too weak to explain the spatial distribution.

Hatching success of eggs of successful breeders does not significantly increase with female age. These findings agree with those of other studies (Coulson 1966, Mills 1973). We were unable to acquire any direct measure of relative nesting success since it was difficult to acquire information as to the age of the attendant female at nests that were ultimately unsuccessful.

We attempted to acquire information on gosling survival rates during the first five weeks of life prior to fledging. The data were, however, complicated by various sampling biases and were therefore ambiguous (Finney 1975).

The data show therefore, that although young females are less productive than adults overall, this is almost entirely due to initial differences in clutch size. No difference in their hatching efficiency was detected, although because of the techniques employed, information on relative nesting success or total brood loss is lacking.

Individual variation in age of first breeding has been recorded for many species (see Cody 1971) as has the variation in recruitment rate between seasons (e.g. Gannets [*Morus bassanus*], Nelson 1966; Red-billed Gulls [*Larus novaehollandiae*], Mills 1973). Return rate data presented in this paper indicate differences between year-classes as such with respect to the age that they will first breed. Thus it appears that, in 1973, a higher proportion of the 2-year-old age-class was nesting than was the case for 3-year-olds.

The maximum number of recruits entering the breeding segment of the population will be influenced by the availability of nesting sites, or other critical resources, in that year. This, in turn, will depend on adult mortality during

the previous year and habitat condition. Since this number usually is smaller than the number of potential recruits, competition for these available positions will ensue. Yearly variations in recruitment ratios have generally been attributed to differences in competitive pressures for essential resources (Pitelka et al. 1955, Cooch 1958, Mills 1973). Differences in year-class recruitment rates imply variations in their competitive ability or the intercession of other factors which may inhibit birds of particular age-classes from even attempting to breed when two or three years old. Assuming no genetic differences, factors that may be of importance are: (1) egg quality such as amount and quality of yolk, (2) pre-fledging development, again as affected by nutrition (Harwood 1975), and (3) conditions on the wintering ground.

In 1971, because of extremely poor conditions while nests were being started, only half the usual number of goslings were feeding in the area. Assuming that food resources did not differ markedly between seasons, it is possible that these goslings were better nourished during the critical post-hatch development period. This may explain why such a high proportion of this year-class bred in 1973 in their second year while relatively fewer of the 1970 year-class were breeding as 3-year-olds in the same year. However, no data on relative development rates of the goslings between years are available and the causes of year-class differences remain speculative.

In attempting to explain the lower reproductive commitment of inexperienced birds, the following considerations appear most relevant:

(1) In an environment where reproductive success is variable, deferred maturity and long life will be favored (Murphy 1968).

(2) Learning may be developed as a mechanism by which susceptibility to environmental fluctuations is decreased for species that breed repeatedly, particularly in those instances where life span is increased and maturity deferred. This may apply to any behavior as long as fitness is increased through different means for different environmental situations.

(3) Selection will favor physiologically mature females who attempt to breed as early as possible, provided that their gain in fitness, which depends on their clutch size and their probability of success, exceeds a loss in fitness incurred due to impairment of future reproductive output through, for example, decreased probability of surviving until the next breeding season (Williams 1966, Cody 1971).

(4) In an environment which is viewed as

unpredictable by the species, the habit of breeding at various ages will be favored over the habit of always breeding at the same age.

We believe, therefore, that the lower reproductive output of first-time breeders is an adaptation for increasing their lifetime fitness. This is contrary to the view that young females are simply not physiologically in tune, an argument which was convincingly refuted by Lack (1968). The ways in which the above-mentioned points may combine to cause the age-specific differences were discussed in detail by Finney (1975).

An important proximate factor regulating clutch size in Snow Geese is the amount of nutrient reserves which a female acquires in northward migration (Ryder 1970, Ankney 1974). Perrins (1965, 1974) suggested that lack of experience in finding food during egg laying by young Great Tits accounted for their smaller clutches and delayed timing relative to adults. Feeding efficiency is thus viewed as both the proximate and the ultimate factor regulating clutch size according to this hypothesis. It also implies that for Great Tits, the most variable environmental factor, and thus implementing learned capabilities to the greatest degree, is food supply during nesting.

For grazing species such as geese, it seems improbable that feeding efficiency is the behavior most affected by experience. This is particularly true of a species such as the Snow Goose where nutrient reserves are accumulated on migration under relatively stable environmental conditions compared to their Arctic breeding grounds. Other aspects of the breeding cycle, such as nest site selection and nest and brood defence, could well be more influenced by experience. If one wishes to ascertain empirically the ultimate factors in clutch size regulation, it is not sufficient simply to show that young birds acquire less nutrient reserves or feed less intensively than adults.

Unfortunately, critical data bearing on the role of experience in the nesting of the Snow Goose are still unavailable and will be difficult to acquire. Although we have been able to document the effect of female age and to discuss some evolutionary implications of the observed pattern, the factors involved in the regulation of reproductive output remain undetermined.

## SUMMARY

An intensive banding program over several years at La Pérouse Bay, Manitoba, has established a marked population of female Snow Geese of known age.

Some females begin nesting as 2-year-olds but others delay first nesting until at least 4 years of age. Year-class differences seem to occur in the average age of recruitment to the nesting segment and in the pattern of return. Differences in the availability of nutrients to goslings may influence subsequent performance of a year-class.

Young females nest predominantly in areas of the colony which were recently colonized or irregularly available for nesting. Nest density is lower where young birds are concentrated.

Young females nest later than adults and clutch size is lower. Difference between year-classes in the timing and clutch size of 3-year-old females suggests that experience, as well as age itself, may be a factor.

Young birds do not have smaller clutches simply because of where they nest or when they nest relative to adults. Even in areas of the colony dominated by young birds, adults nest earlier and have larger clutches.

Average clutch size decreases as the season progresses. This relationship holds when single age classes are examined, showing that the relationship is not an artifact of the age structure of the population.

Consideration of the selective pressures which could result in deferred maturity and lower clutch sizes among young nesting females leads to the conclusion that experience must be a factor. Feeding efficiency is not likely to be the critical factor requiring learning in this grazing species. The nutrient reserves of a young female upon arrival at the nesting colony are likely to be low relative to adults, although this has yet to be demonstrated. Although body condition may act as the proximate factor influencing clutch size and timing, the ultimate factors upon which selection acts may be different. Future studies will have to determine both the mechanisms and causes of the reproductive regulation for the species.

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