

## Female age and egg size in the Lesser Snow Goose

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We studied the relationship between female age and egg size of the Lesser Snow Goose *Anser caerulescens caerulescens* at La Pérouse Bay, Manitoba, Canada, over a period of 15 years (1976–90). Two and three years old birds laid significantly lighter eggs than the rest of the population in a given year, laying sequence and clutch size. Analysis of repeated measures of individual birds showed equivalent results. Younger birds also laid eggs which were significantly longer and thinner than eggs laid by older birds. The pattern of intraclutch egg size variation was the same in both young and old birds, with younger birds laying slightly smaller eggs in each position within the laying sequence. Some physiological maturation process was probably responsible for the smaller eggs younger birds laid because the pattern held within individuals. However, changes in egg size and shape may be due to breeding experience rather than age itself. We detected no evidence for age-specific differences in egg size of older birds. Thus, neither senescent declines in egg size nor an increased allocation of reserves to reproduction appear to be occurring in this species.

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Long lived birds are not only faced with the decisions regarding current reproductive effort but also future reproductive efforts (Williams 1966). As an individual ages, allocations to reproduction and survival should change in their relative proportions to maximize lifetime reproductive output (Pianka and Parker 1975). Both sampling a population at a given time and monitoring individuals through time can provide insight into how a population changes its life history strategies with age. However, the latter studies have the advantage of controlling for the possible effects of differential mortality on individuals pursuing a certain type of life history strategy (Curio 1983). Another important component in the analysis of age-specific life-history strategies, especially in species with significant age-structure, are the confounding effects of developmental age and experience. In many species, fecundity increases with age to some point. Such changes may reflect increased reproductive experience (e.g., Hamann and Cooke 1986). Alternatively, such changes may reflect age-specific expressions of a given reproductive trait (Pugesek 1981, 1984, but see Nur 1984).

We examined the pattern of age-specific variation in egg size in a colonial species of an avian herbivore, the Lesser Snow Goose *Anser caerulescens caerulescens*, breeding at La Pérouse Bay, Manitoba, Canada (58°44'N, 94°28'W). Clutch size is known to increase and laying date to become earlier up to age five in this species (Finney and Cooke 1978, Hamann and Cooke 1986). Rockwell et al. (1993) recently analyzed the effects of age on total reproductive output of Lesser Snow Geese. Geese were able to lay more eggs, and improved their ability to rear young and avoid nest failure, up to age six. This probably reflects an increase in breeding experience and possibly a maturation process. After age six, hatchability of eggs declined and total brood failure increased. This was attributed to physical senescence of the older birds and the breeding site philopatry of old birds to a brood rearing ground declining in quality (Rockwell et al. 1993).

The selective advantage of laying large eggs has been shown in some birds, most notably seabirds (Nelson 1988). However, most species show a great range in egg size. Larger eggs may be selected for if the young that

hatch from them are larger or heavier and can withstand periods of cold and/or food shortages (Ankney 1980, Thomas and Peach Brown 1988). Younger females may not be able to lay large eggs so their young will be at a disadvantage. This may be due to a lack in experience in gaining the necessary reserves to lay their eggs or due to a physiological restriction. Alternatively, a female may lay smaller eggs at a young age so as not to compromise her future reproductive effort. Therefore, it may be adaptive for the female to lay small eggs while she is still young. These hypotheses all assume that egg production is costly to females. In arctic breeding birds, there are no, or little, nutrients available to them at the breeding grounds so laying eggs will have at least some cost in expended reserves (Ryder 1970). Variation in egg size is also seen within clutches of individuals (Slagsvold et al. 1984). This pattern is assumed to be adaptive because it partitions nutrients to the eggs most likely to survive to fledging (Williams et al. 1993). However, the within individual variation in egg size may not be adaptive (Amundsen and Stokland 1988, Robertson and Cooke 1993).

In this paper we describe the age-specific pattern of egg size in clutches of Snow Geese. We are also able to show how individuals display change in their mean egg size as they age. The effects on the intraclutch size pattern are also described to determine if this pattern is different in younger birds. Finally, we explore the potential proximate and ultimate causes of these age-specific patterns of egg size in Snow Geese and compare the pattern with those of other species.

## Methods

The data were collected as part of a long term study on Lesser Snow Geese at La Pérouse Bay, over the years 1976–1990. General field methods are described in Finney and Cooke (1978) and Cooke et al. (1985). Each year, approximately 300 nests are monitored daily from the initiation of laying to the completion of the clutch. Each new egg found in the nest during these daily searches is individually numbered and weighed, with a spring Pesola, to the nearest gram. In 1984–86 lengths and maximum breadths of eggs were also measured with calipers to the nearest  $\pm 0.1$  mm. Nests are visited daily until incubation, and then they are not disturbed until hatch. At hatch an additional 800–1000 nests are monitored. At the time of hatch, mass of all hatching eggs is measured to the nearest gram. Approximately 5 weeks after hatch, the adults moult their flight feathers, and are temporarily flightless. During this period, approximately 4000–6000 adults and goslings are rounded up, aged, sexed and ringed. Females ringed as goslings which return to breed at the colony comprise the sample of known-age adult females used in our analysis.

We used ANOVA to test for significant variation in both the mass and dimensions of eggs laid by adult

females of different ages. Because egg mass in this population varies significantly as a function of year, laying sequence and clutch size (Williams et al. 1993), all three factors were included as categorical variables in analyses of variation of egg mass at the time of laying. To eliminate statistical problems caused by the presence of multiple eggs from each nest in analyses which included eggs of different laying sequences, we selected a single egg at random from each nest for which age of the attendant female was known. While this approach is perhaps not as robust as one which incorporated all the repeated measures (i.e., each egg within a clutch) for individual birds, it did eliminate the significant complications of (a) variable number of eggs among individuals within a given year for which both mass at laying and sequence were known, and (b) variable number of years of clutch and egg size data for individual birds. To confirm that the results of these analyses were not dependent upon the particular eggs included in the randomly selected data, we repeated the analyses 25 times. We report the mean and range of values of the various sums of squares and F-statistics.

For analyses of within-individual changes, we did not have a sufficient sample of birds with repeated measures of fresh egg mass. Thus, we used available data for egg mass at time of hatching. Egg mass at hatch is highly correlated with egg mass at time of laying (Lessells et al. 1989). Since laying sequence of eggs cannot always be precisely inferred from hatching sequence, we could not control for laying sequence in this analysis. However, since there was no significant interaction of laying sequence with age in our analysis of the population sample, our inability to control for laying sequence should not affect our overall results, provided the sample of eggs at hatch is random with respect to true laying sequence. Because of the sparse structure of the data matrix (which included a large number of missing values corresponding to years in which egg mass for a given individual was not recorded – generally because they were not observed nesting), we did not include year explicitly as a factor in the analyses of individual birds. However, to control for variation due to sampling year, egg mass was expressed as a deviate from the overall annual mean (across all age classes).

In all analyses, the variation contributed by the main Age effect was further analyzed by decomposing the main effect sums of squares into a series of a posteriori contrasts to test specific hypotheses that were suggested by preliminary analysis of the data. Significances of multiple non-orthogonal tests were determined using a sequential Bonferroni adjustment with a tablewide significance of  $\alpha = 0.05$ , to control for the overall probability of declaring differences to be significant by random chance (Rice 1989).

Table 1. Analysis of variation in fresh egg mass of Lesser Snow Geese as a function of year (1976–1990), laying sequence (1–4), clutch size (2–6) and age of adult female (2–14 years).

Reduced model<sup>a</sup>

Source	df	SS <sup>b</sup>	F (range) <sup>c</sup>	P
Year	13	2469.25	2.53 (1.82–2.86)	0.006
Sequence	3	732.55	3.26 (1.74–5.59)	0.062
Clutch size	4	1114.49	3.71 (1.95–5.86)	0.022
Age	12	1736.77	1.93 (1.32–2.60)	0.051
CS × S	9	1644.82	2.35 (1.05–4.93)	0.059
Error	773	58053.13		

<sup>a</sup> Final model after backwards elimination of non-significant terms from the fully saturated model.  $\alpha$  for removal of interaction term = 0.15.  $\alpha$  for removal of main effect = 0.05.

<sup>b</sup> Mean partial (Type III) SS (SAS Institute 1990) for 25 different subsets of randomly selected eggs (one from each nest).

<sup>c</sup> Mean F-statistic for 25 different subsets of randomly selected eggs (one from each nest). Means are given with range of F-statistics from random subsets. Significance estimated from mean F-statistic.

Table 2. Analysis of variation in fresh egg mass of Lesser Snow Geese as a function of year (1976–1990), laying sequence (1–4), clutch size (2–6) and age of adult female.

#### 1. Young birds (2–5 years)

Source	df	SS <sup>a</sup>	F (range) <sup>b</sup>	P
Year	13	717.95	0.70 (0.44–0.96)	0.774
Sequence	3	876.76	3.77 (0.82–8.68)	0.096
Clutch size	4	461.11	1.48 (0.91–2.75)	0.249
Age	3	703.70	2.99 (1.94–4.32)	0.047
Linear <sup>c</sup>	1	518.17	6.61 (1.99–10.3)	0.026*
2 vs 3 <sup>d</sup>	1	77.13	0.98 (0.01–2.46)	0.408
3 vs 4 <sup>e</sup>	1	236.83	3.03 (0.80–6.97)	0.133
4 vs 5 <sup>f</sup>	1	43.58	0.55 (0.01–1.65)	0.541
Error	277	21818.82		

#### 2. Old birds (>4 years)

Source	df	SS	F (range)	P
Year	13	2103.87	2.19 (1.73–2.82)	0.018
Sequence	3	583.66	2.61 (0.65–4.32)	0.123
Clutch size	4	1097.92	3.71 (2.13–5.71)	0.013
Age	9	1047.32	1.58 (0.57–2.39)	0.177
Linear <sup>c</sup>	1	166.67	2.27 (0.80–4.62)	0.165
CS × S	9	1731.28	2.59 (1.45–4.44)	0.035
Error	590	43715.27		

<sup>a</sup> Mean partial (Type III) SS (SAS Institute 1990) for 25 different subsets of randomly selected eggs (one from each nest).

<sup>b</sup> Mean F-statistic for 25 different subsets of randomly selected eggs (one from each nest). Means given with range of F-statistics for random subsets. Significance estimated from mean F-statistic.

Decomposition of main effect (Age) into a posteriori means comparisons (Sokal and Rohlf 1981).

<sup>c</sup> young birds:  $H_0: -3\mu_2 - \mu_3 + \mu_4 + 3\mu_5 = 0$ , old birds:  $H_0: 9\mu_5 - 7\mu_6 \dots 7\mu_{13} + 9\mu_{14} = 0$ ;

<sup>d</sup>  $H_0: \mu_2 = \mu_3$ ;

<sup>e</sup>  $H_0: \mu_3 = \mu_4$ ;

<sup>f</sup>  $H_0: \mu_4 = \mu_5$ .

\*  $P < 0.05$  at tablewide level.

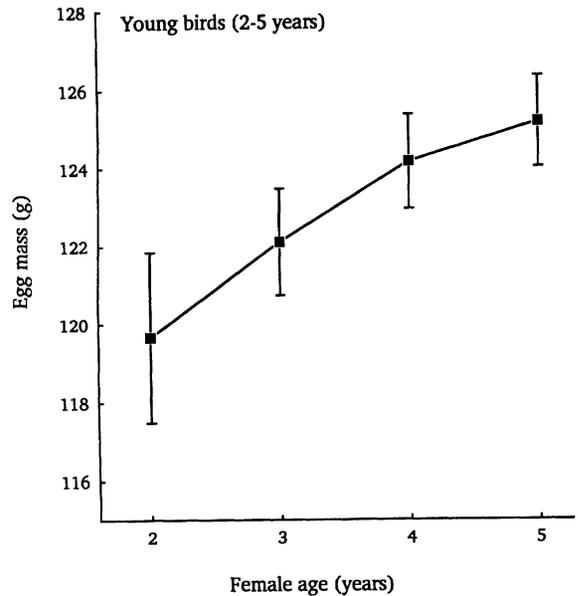


Fig. 1. Variation in mean egg mass at laying with age among younger (age 2–5 years) adult female Lesser Snow Geese, 1976–1990. Means and standard errors estimated as least-square means (PROC GLM; SAS Institute 1990) from ANOVA controlling for year, clutch size and laying sequence (Table 2). Sample sizes:  $n_2 = 22$ ;  $n_3 = 70$ ;  $n_4 = 94$ ;  $n_5 = 115$ .

## Results

### Age and egg mass – population sample

Among eggs randomly selected from 815 nests from 14 years for which the age of the adult female is known (2–14 years), egg mass varied significantly with female age for a given year, clutch size and laying sequence (Table 1). There was no significant interaction of age

Table 3. Repeated measures analysis of variation in egg mass at hatch among young (age 2–5 years) adult female Lesser Snow Geese as a function of age, 1976–1990.

Source	df	F <sup>a</sup>	P
Age	3	6.26	<0.001
Linear <sup>b</sup>	1	15.78	<0.001*
2 vs 3 <sup>c</sup>	1	4.58	0.034
3 vs 4 <sup>d</sup>	1	7.58	0.007*
4 vs 5 <sup>e</sup>	1	0.00	0.991

<sup>a</sup> F-statistics calculated using maximum likelihood estimates from unstructured covariance model with missing values (PROC MIXED; SAS Institute 1990).

Decomposition of main effect (Age) into a posteriori means comparisons (Sokal and Rohlf 1981):

<sup>b</sup>  $H_0: -3\mu_2 - \mu_3 + \mu_4 + 3\mu_5 = 0$ ;

<sup>c</sup>  $H_0: \mu_2 = \mu_3$ ;

<sup>d</sup>  $H_0: \mu_3 = \mu_4$ ;

<sup>e</sup>  $H_0: \mu_4 = \mu_5$ .

\*  $P < 0.05$  at tablewide level.

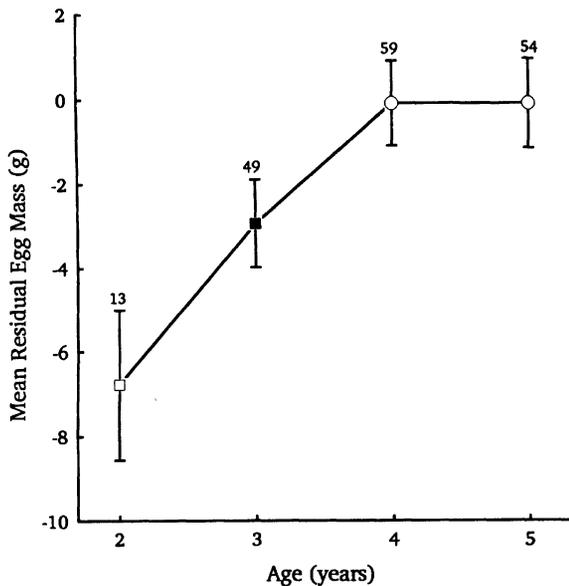


Fig. 2. Age-specific variation in mean egg mass at hatch of young (age 2–5) adult female Lesser Snow Geese for which multiple observations were available. Means and standard errors estimated as least-square means (PROC GLM; SAS Institute 1990) from repeated-measures ANOVA with unstructured covariance matrix. Sample sizes reflect number of observations within an age-class.

with either year, clutch size or sequence. Thus, the relationship of egg size and sequence did not differ significantly among age classes or years (although our ability to detect such interactions may have been somewhat reduced by our analytical approach – see Methods).

When the relationship between age of the adult female and egg mass was partitioned between younger and older females, there was highly significant variation in egg mass among age classes for younger birds, but there was no evidence of age-specific differences in egg mass among older birds (Table 2). The age partitions were chosen based on previous observations that clutch size increases significantly with age to age 5, and is independent of age thereafter (Rockwell et al. 1993). Birds 5 years of age are included in both sets. Although a posteriori paired comparisons among consecutive age-classes for younger birds did not reveal significant differences in egg mass, a test for linear increase in egg mass with age was significant (Table 2, Fig. 1). A similar test for a linear change in egg mass among older birds was not significant.

### Age and egg mass – individual birds

To control for the possibility that the observed age-specific changes in egg mass may reflect peculiarities of sampling at the population level, we also examined the pattern of age-specific variation in egg mass for birds for

which repeated measures were available. Since there was no evidence of significant variation in egg mass with age among older birds, we restricted our analysis to birds from 2–5 years of age.

Among 175 young adult females for which repeated measures of egg mass at hatch were available, egg mass

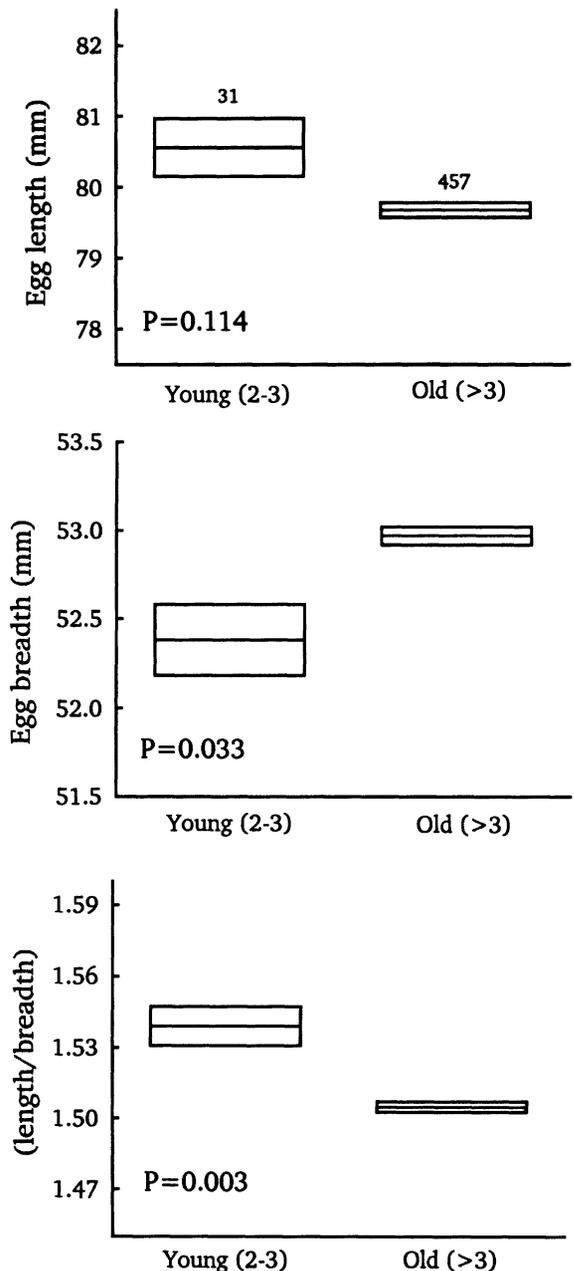


Fig. 3. Difference in mean egg length, breadth, and the ratio of (length/breadth) among young (age 2–3 years) and old (age > 3 years) adult female Lesser Snow Geese, 1984–1986. Means and standard errors estimated as least-square means (PROC GLM; SAS Institute 1990) from ANOVA controlling for year, and are given with sample sizes.

varied significantly with age (Table 3). There was a marginal difference in egg mass between 2 and 3 year-old birds (not significant at tablewide level), a significant difference between 3 and 4 year-old birds, and no significant difference between 4 and 5 year-old females (Table 3, Fig. 2).

### Age and egg dimensions – population sample

Since 2 and 3 year-old birds tended to lay significantly lighter eggs than older birds for a given year and laying sequence, we tested for age-specific differences in size of the egg (length, breadth, and ratio of length to breadth). Mean egg length was longer in 2 and 3 year old birds (although not quite significant), while the mean egg breadth of young birds was significantly slimmer (Fig. 3).

## Discussion

A wide variety of patterns in egg size varying with age have been documented. Increases in egg size with age (Weimerskirch 1990, Williams 1990); reductions in egg size with age (Shaw 1986, Reid 1988) and even cases where egg size increases to a point and then decreases with age (Hamer and Furness 1991), have all been shown. Examples of no age effect on egg size have also been documented (Erikstad et al. 1985, Hepp et al. 1987, Järvinen and Pryn 1989). In Snow Geese, egg mass increases significantly with age from 2 to 5 years, both at the population level and within individuals, with no significant differences among birds >5 years of age. There was also a significant difference in the shape of eggs as Snow Geese age.

The selective advantages of early laying (Cooke et al. 1984) and large clutch size (Rockwell et al. 1987) have been clearly demonstrated in Snow Geese. The selective regime on egg size is less clear (Ankney and Bisset 1976, Cooke et al. 1991). Hatchability and subsequent fledging success are not functions of egg size but rather laying sequence (Williams et al. 1993) in Snow Geese and no effect of egg size or laying sequence was seen in Canada Geese *Branta canadensis* (Leblanc 1987a). This apparent lack of selection for large eggs plus the absence of a detectable phenotypic trade-off between clutch size and egg size (Lessells et al. 1989) suggest that egg size may not be under directional selection in Snow Geese. We have shown that younger geese lay smaller eggs, but the lower reproductive success of young Snow Geese is due to their smaller clutch sizes and their susceptibility to total nest failure (losing a nest to a predator or abandoning the nest; Rockwell et al. 1993, Williams et al. 1993). Since clutch size (Cooch et al. 1992) and most likely total nest failure are independent of egg size, the lower reproductive output of young Snow Geese is probably not due to the smaller eggs they lay.

The question of why younger geese lay smaller eggs is probably best explained on a proximate level. By showing that individual geese increase the size of the eggs they lay after the ages of two and three, we can conclude two things. First there is no evidence, at the population level, that there is differential mortality of young birds which lay smaller eggs (Curio 1983). The second point is that since the increase occurs within individuals, some form of maturation process is likely to be involved.

Two not mutually exclusive types of maturation processes could be involved; the young birds could be laying smaller eggs because they are physiologically unable to lay an 'adult' sized egg (age-specific expression of the trait) or the young birds are not able to acquire enough nutrient reserves to lay larger eggs (experience). In the La Pérouse Bay population we are unable to determine precisely whether or not a given bird breeds in a given season. Thus, we cannot directly differentiate the 'maturation' versus 'experience' hypotheses for most of our data. However, in studies where birds are supplementally fed, in general, egg size does not increase with supplemental feeding (Arnold et al. 1991, Arnold 1992, Van Klinken 1992) or the results were ambiguous (Bolton et al. 1992, Nilsson and Svensson 1993). In addition, the pattern of length and breadth of eggs suggest that on some level a physiological/anatomical restriction is reducing the egg size of younger birds. Our results were similar to those reported by Syroechkovskiy (1979), in that young geese lay longer and slimmer eggs. This pattern was also documented in Ural Owls *Strix uralensis* (Pietiäinen et al. 1986). Parsons (1976) proposed that the slimmer "a-egg" of Herring Gulls *Larus argentatus* could be due to an initial inelasticity of the oviduct; after the first egg has passed the oviduct is sufficiently stretched to allow eggs of greater breadth to be produced. Similar patterns have been seen in Canada Geese (Leblanc 1987b), and Common Eiders *Somateria mollissima* (Robertson and Cooke 1993), in that the first egg of a clutch is generally long and slim. It is possible to extend this hypothesis to not just the first egg of the breeding season but to the first eggs of a bird's life. We propose that in younger geese, owing to initial oviduct inelasticity, albumin is deposited preferentially along the length rather than the breadth axis, but not as much to lay an egg of 'adult' size. From a regression of egg mass on length and breadth (F. Cooke, unpublished data), a reduction in 1 unit of breadth requires a 2.9 increase in length for the egg to maintain the same mass. It may be that to completely compensate for the loss in mass in the breadth the egg would have to be excessively elongated and other factors like hatchability, surface to volume ratios and structural integrity, would be compromised.

The within-clutch pattern of egg-size variation is similar in older and young birds, suggesting that the selective or physiological processes discussed in Williams et al. (1993) are present for younger and older geese alike. Therefore, an abnormally small egg at some laying sequence is not causing the reduction in egg size of younger

birds. Others have found that the within-clutch pattern of egg-size variation was different in younger birds. In Coots *Fulica americana*, Crawford (1980) found that eggs of yearlings were smaller, although not significantly so, because the first five eggs of the clutch were very short. After the fifth egg, however, the young Coots were able to lay 'adult' sized eggs.

We did not detect any evidence of senescence in egg size of Snow Geese. Kear and Berger (1980) found that eggs of female Hawaiian Geese *Branta sandvicensis* decreased in size after age five. We are not sure why Hawaiian Geese show such a reduction in egg size so early in life; it may be due to their unique ecological conditions. A few Snow Geese do, however, live well into their twenties and it may be that in these birds evidence of senescence may be found. Rockwell et al. (1993) did find evidence of senescence in Snow Geese. Eggs of older geese had a lower chance of hatching than those of younger geese. It could be that the senescence is manifested in the quality of eggs and not the amount of total reserve allocated to the egg. Species which have been shown to have a reduction in egg size with age, tend to have a survival value (Bolton 1991), unlike Snow Geese (Cooke et al. 1991, Williams et al. 1993), and Canada Geese (Leblanc 1987a).

We have documented the pattern of age-specific egg size in Lesser Snow Geese. Although the pattern does somewhat qualitatively support an increase in reproductive effort with age (Charlesworth 1980), other evidence suggests that the observed pattern is best explained by a physiological/anatomical maturation of young birds until they are able to lay full-sized eggs.

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