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LONG-TERM DECLINE IN BODY SIZE IN A SNOW GOOSE POPULATION: EVIDENCE OF ENVIRONMENTAL DEGRADATION?

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SUMMARY

(1) The effect of environmental factors on annual body size variation was investigated in a breeding population of lesser snow geese (*Anser caerulescens caerulescens* L.) La Pérouse Bay, Manitoba, using data from 1969 to the present. The population size has increased from approximately 2000 to 10000 pairs during this period (Cooch *et al.* 1989).

(2) Annual mean gosling body mass, tarsus and culmen length (measured at fledging) declined significantly by approximately 16% (240 g), 4% (3.4 mm), and 2% (0.93 mm) respectively in cohorts hatching between 1976 and 1988. The decline in gosling size has led to a significant decline in size of locally bred adults. Annual mean adult female body mass, tarsus and culmen lengths declined by approximately 15% (270 g), 6% (5.4 mm), and 4% (2.3 mm), respectively, in cohorts hatching between 1969 and 1986.

(3) Gosling growth and subsequent adult size was also reduced in years with cold, wet weather after hatch.

(4) The decline in gosling size was not dependent on the pattern of annual variation in egg or hatch mass, nor systematic changes in annual mean hatch date or post-hatch weather. Goslings reared by individual adult females showed a decline in size over time, suggesting that the general decline reflects a non-genetic change in gosling growth rates during the fledging period. The most probable non-genetic factor is a long-term reduction in food available to the geese at La Pérouse Bay. This reduction in food availability may reflect over-exploitation of primary food plants by the geese.

INTRODUCTION

Body size has measurable phenotypic variation in several species of birds (Boag & van Noordwijk 1987, and references contained therein), and can have significant effects on both survival (Perrins Harris & Britton 1973; Harris & Rothery 1985; Newton & Moss 1986; Owen & Black 1989; Conroy, Costanzo & Stotts 1989) and

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fecundity (Ankney & MacInnes 1978; Lessells 1982; Murphy 1986). Although there is, in general, a significant genetic component to body size variation in birds (Boag & van Noordwijk 1987), there is also a significant environmental component (James 1983; van Noordwijk, Van Balen & Scharloo 1988; Richner 1989).

In several species of herbivorous arctic-nesting geese there is typically a significant seasonal decline in gosling growth rates and little evidence for compensatory growth (Cooch *et al.* in press; Sedinger & Flint, in press; K. Larsson & P. Forslund, unpublished). Thus, late hatching goslings with slower growth rates show significantly reduced adult size. In lesser snow geese, this decline is independent of the genotype of the parent, and represents seasonal differences in the environmental component of gosling growth rates (Cooch *et al.*, in press). Both intra-seasonal differences in foraging behaviour (Sedinger & Raveling 1988; Sedinger & Flint, in press) and food-plant quality and quantity (Sedinger & Flint, in press; K. Larsson & P. Forslund, unpublished) have been proposed as the proximate mechanisms for the reduced growth rates of late hatching goslings. Although the different hypotheses may simply reflect species differences in aspects of the breeding biology, both assume variation in the per capita availability of primary food plants and proportionately lower nutritive intake by late hatching goslings.

Food availability may vary significantly among years due to differences in the weather (which might influence both plant and gosling growth) and the demography of the goose population. There has been a significant increase over time in the number of geese utilizing La Pérouse Bay (Cooch *et al.* 1989), and a decline in the availability of food on the traditional foraging areas. This has also been documented at another snow goose colony (Kerbes, Kotanen & Jefferies 1990). Both factors may significantly affect the pattern of annual variation in body size, and are examined in this study.

METHODS

Data on the breeding biology of the lesser snow goose have been collected annually at La Pérouse Bay, Manitoba (58°4'N, 94°4'W) from 1968 to 1989. The colony has increased significantly in size since 1968 (Cooch *et al.* 1989), presently numbering 10 000–12 000 breeding pairs. General field methods are described in Finney & Cooke (1978) and Cooke *et al.* (1985).

Approximately 2000 nests are monitored at hatch each year. Eggs are weighed to the nearest gram at the time of hatch. Hatching goslings receive a uniquely numbered web-tag, allowing tagged individuals to be aged precisely during annual ringing drives (age=days since hatch), and matched to specific nests and parents. All adults and goslings are individually marked with cohort-specific rings during post-breeding ringing drives involving 4000–7000 geese annually. All web-tagged goslings, and a sample of known-age adults are weighed and measured during the ringing drives. Details of the measurements taken from all birds are described in Davies, Rockwell & Cooke (1988).

Size measurements

In this paper we examined two aspects of size variation: body mass and structural size. Body mass was the mass (g) recorded for both goslings and adults at ringing.

For adults, we followed the suggestion of Alisauskas & Ankney (1990), and derived a separate structural size index by extracting the first principal component from the correlation matrix of head length (mm), culmen length (mm) and tarsus length (mm). For correlated variables, PC1 explains most of the variance when factor loadings are approximately equal and positive, and is commonly used as an index of structural size (Alisauskas & Ankney 1987; Moser & Rusch 1988; Rising & Somers 1989; Freeman & Jackson 1990; Alisauskas & Ankney 1990). Factor loadings for PC1 were 0.42, 0.64 and 0.65 for tarsus, culmen and head length, respectively, and explained 68% of the observed variation in these characters. Head length was not measured for goslings in early years. Thus, we examined variation in the structural size of goslings by analysing tarsus and culmen length separately. Because gosling growth is linear over the range of ages of goslings measured at ringing (Cooch *et al.*, in press), differences in size of goslings at any given age reflect differences in the linear growth rates of those goslings. Thus, differences in gosling size (at a given age) and gosling growth rates are equivalent, and the terminology is used interchangeably in the text where appropriate. All gosling measurements were adjusted for differences due to age in days and sex before further analysis (Cooch *et al.*, in press).

Data set restrictions

All known-age (age=days since hatch) goslings and a sample of known-aged adults (age=years since hatch) recaptured during annual ringing drives since 1976 have been measured. Lesser snow geese show strong female philopatry, and virtually all of the adult males at La Pérouse Bay were hatched at other unidentified colonies (Cooke, MacInnes & Prevet 1975). Therefore, all analyses were restricted to females only. For statistical reasons, only a single, randomly selected individual female was chosen from each brood for all analyses of both goslings and adults (details in Cooch *et al.*, in press). Only birds for which the potentially confounding factors of hatch date, age (days post-hatch for goslings; years post-hatch year for adults) and brood size (for goslings) were known precisely were included (Davies, Rockwell & Cooke 1988; Cooch *et al.*, in press). Although the adult size data for the 1969–72 cohorts did not meet these criterion for analysis, they were included in the data set used to calculate the structural size index (PC1), and are presented in the figures. Because hatch date and brood size are independent for broods reared by adult females age ≥ 4 years post-hatch year (E.G. Cooch, D.B. Lank, R.F. Rockwell & F. Cooke, unpublished), only goslings from nests of older adult females were used to eliminate the problem of highly correlated variables in multivariate analyses. All gosling measurements were adjusted for differences due to age in days by simple linear regression (Cooch *et al.*, in press). Within a year, only the first record for each gosling was used to eliminate biases due to multiple recapture of the same bird. For adults with multiple measurements in different years, a single record was chosen at random.

Potential environmental correlates

Nesting chronology and brood size

Within a season, growth rates of goslings from early hatching nests are significantly

greater than those of goslings from relatively later hatching nests, and significantly greater for goslings from relatively larger broods (Cooch *et al.*, in press). Both factors are part of the environmental component of size variation in this species (Cooch *et al.*, in press).

There may be significant variation in the quantity and quality of food available to the geese at the breeding site related to annual differences in chronology. Therefore, we included annual mean hatch date as a factor in analyses of both adult and gosling size variation.

Weather

Although the annual mean post-hatch weather was not significantly correlated with annual differences in timing of nesting at La Pérouse Bay ($r = 0.141$, d.f. = 12, $P = 0.645$ – means calculated from hatch date and post-hatch weather for gosling sample), weather variation is known to influence growth rates in a number of species of birds (Skagen 1987; Rofstad 1988; Beintema & Visser 1989; Donazar & Ceballos 1989; Konarzewski & Taylor 1989; Cruz & Cruz 1990). Poor weather may reduce energy available for growth by increasing the energy expenditure of goslings attempting to maintain body heat. It may also cause increased brooding by the parents, which may significantly reduce foraging time and food intake. Weather may also influence gosling growth rates indirectly through effect on variation in the annual production of food plants. Annual production of the primary food plants of lesser snow geese is likely to be influenced by precipitation and temperature in the preceding year (R. Harmsen, pers. comm.). We can test for both possibilities by performing all analyses of body size with both weather in any given year and the preceding year.

We examined the effect of post-hatch period weather on the growth rates of individual birds. Because the majority of growth in lesser snow geese occurs prior to fledging (Cooch *et al.*, in press), the post-hatch period was defined as the interval between the date of hatch and 5 weeks post-hatch for each gosling. Daily mean temperature and total rainfall recorded at the meteorological station at Churchill Airport were used. The data were reduced to a single weather index by extracting the first principal component for the post-hatch period for each individual bird. The factor loadings were of equal magnitude and opposite sign (-0.707 total rainfall; 0.707 mean temperature). Thus, large positive values of the weather index reflected warm, dry weather, while large negative values reflected cold, wet weather.

RESULTS

Annual variation in gosling growth rates

We examined the effects of timing, brood size, weather and cohort on variation in sizes of a sample of 1774 female goslings from nests of older adult females (age ≥ 4) measured at fledging (see Methods). The analyses used partial (Type III) sums of squares (SS), which simultaneously control for the effect of all other terms entered into the model (SAS Institute 1985). Because there was no significant correlation among any of the independent variables, all terms were included in the model, with all possible interaction terms. In separate analyses, cohort was treated as both a linear and a categorical variable. We report the most significant result. All other terms were entered as linear variables.

TABLE 1. Multiple regression of gosling size in lesser snow geese (1976–88 cohorts)

Measurement	Term	<i>F</i>	<i>P</i>	Sign
Body mass	Hatch date ^f	45.17	<<0.001	–
	Hatch date ^m	0.11	0.739	–
	Brood size	15.65	<<0.001	+
	Weather	94.74	<<0.001	+
	Cohort	396.91	<<0.001	–
	Model	142.51	<<0.001	$R^2 = 0.29$
Tarsus length	Hatch date ^f	82.01	<<0.001	–
	Hatch date ^m	28.89	<<0.001	–
	Brood size	10.28	0.001	+
	Weather	72.80	<<0.001	+
	Cohort	48.75	<<0.001	–
	Model	40.36	<<0.001	$R^2 = 0.13$
Culmen length	Hatch date ^f	42.63	<<0.001	–
	Hatch date ^m	3.31	0.069	–
	Brood size	7.28	0.007	+
	Weather	144.47	<<0.001	+
	Cohort	11.99	0.001	–
	Model	48.02	<<0.001	$R^2 = 0.12$

F-statistics calculated using partial (Type III) SS (SAS Institute 1985). Hatch date^f = relative hatch date within season (*n* days \pm annual mean within a season). Hatch date^m = annual mean hatch date (1 May = day 1). Sample size = 1774 for all analyses. All interaction terms were non-significant, and are not included in the table.

There was a highly significant long-term decline in gosling body mass, tarsus and culmen length, controlling for hatch date, brood size and weather (Table 1; Fig. 1). Gosling body mass, tarsus and culmen length declined by approximately 15%, 4% and 2%, respectively. Controlling for other variables, relative hatch date and brood size, also had significant effects on gosling growth, as shown by (Cooch *et al.*, in press). Although annual differences in mean hatch date did not significantly affect annual variation in gosling body mass, there was a strongly significant decrease in gosling tarsus and culmen length with later mean hatch date. Cold, wet weather significantly reduced growth rates of all three characters. There was no significant influence of weather in the previous year on gosling growth in a given year. There were no significant interactions between any of the variables. The overall proportion of variance explained by the model was low, but highly significant ($R^2 = 0.12 - 0.29$; Table 1).

Goslings that are large at hatching are also larger at fledging (Newell 1988), so the decline in gosling size at fledging may reflect a long-term decline in hatching mass. Annual mean hatching mass measured at the pipping stage has shown significant annual variation from 1976 to 1989 ($F = 2.50$, d.f. = 13,936, $P = 0.002$), but no evidence of a systematic change ($F = 2.27$, d.f. = 948, $P = 0.133$).

Genetic and environmental components

If the long-term decline in body size reflects environmental and not genetic

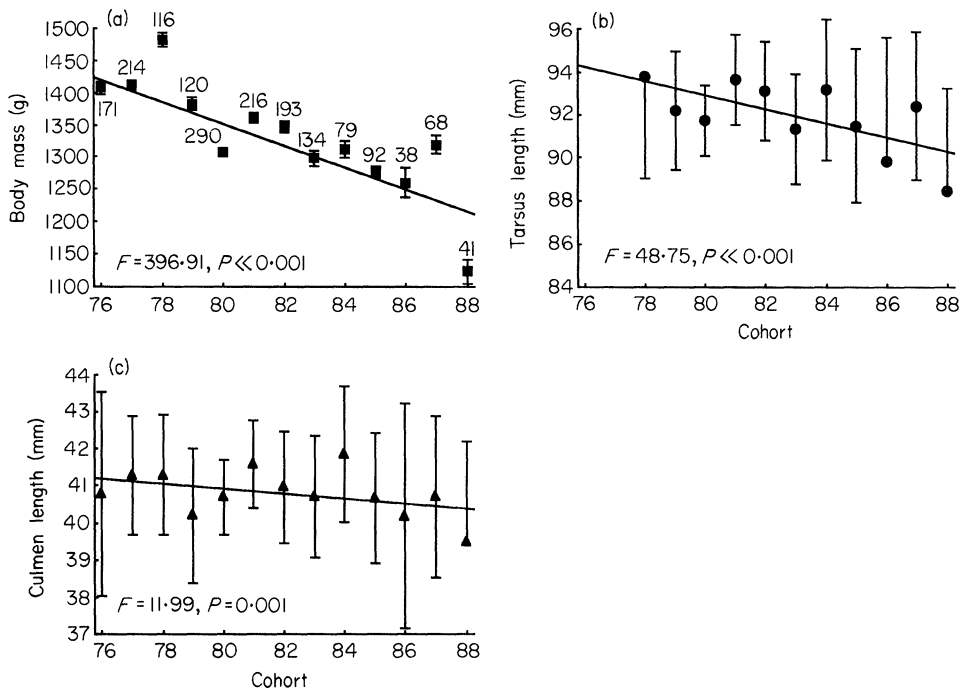


FIG. 1. Regression of gosling size, measured as (a) body mass, (b) tarsus length and (c) culmen length, against year. Annual means calculated as least-square estimates after adjusting size for hatch date, brood size and natal-year weather (see Methods). Mean values plotted with standard error of the mean and sample size.

changes in the population, then we would predict that the goslings reared by an individual female in year t would be larger by some predictable magnitude than goslings reared by that same individual in a later year ($t + n$). As the parental contribution to the gosling genotype remains constant over time in monogamous snow geese, differences in the size of goslings reared by the same individual in two different years most likely reflects differences in the environmental component of growth rate. The problems associated with mate change are outlined in the discussion.

A sample of seventy-three adult females were recorded as having reared broods (subsequently measured at ringing) in at least two different seasons. The sample was restricted to birds more than years old to minimize differences in gosling growth rate that might be related to differences in parental experience. The sizes of goslings for all females in the data set were adjusted by ANOVA for annual differences in hatch date and brood size (Cooch *et al.*, in press; Sedinger & Flint, in press). Individual goslings sizes were then linearly adjusted for variation in post-hatch weather. The remaining variation was attributed to yearly changes. The relative difference in size (expressed as a %) between the first and last record for individual females was calculated, and the difference regressed on the number of years between the two measurements (J.T. Smith, personal communication). All percentages were arcsine transformed prior to analysis (Sokal & Rohlf 1981). As the difference in gosling size must logically be 0 when the number of years between measurements is

0, the regressions were forced through the origin. There was a significant negative difference between the first and last measured goslings reared by individual females for body mass and culmen length (Fig. 2). The change in tarsus length was not statistically significant, but was in the same direction as the other two characters. However, because of the decrease in sample size with greater number of years between records (Fig. 2), and the possible confounding influence of mate change (outlined in the Discussion), this approach may underestimate differences.

An alternative interpretation of these results is that gosling growth rates decline significantly with increasing age of the adult female. Older adult females may do less well than younger females at leading their offspring to optimal foraging locations. Although age and year are logically confounded, partial correlation analysis showed that gosling size was significantly correlated with year when adult female age was held constant (Table 2a), while size and adult female age were not correlated when controlled for year (Table 2b). Thus, there was no evidence that the decline in the sizes of goslings (and ultimately adults) reared by individual females is due to the slower growing late hatching goslings (Cooch *et al.*, in press). Because the adult sample is comprised of a non-random subset of brood sizes (Cooch *et al.*, in press), brood size was not included in the analysis.

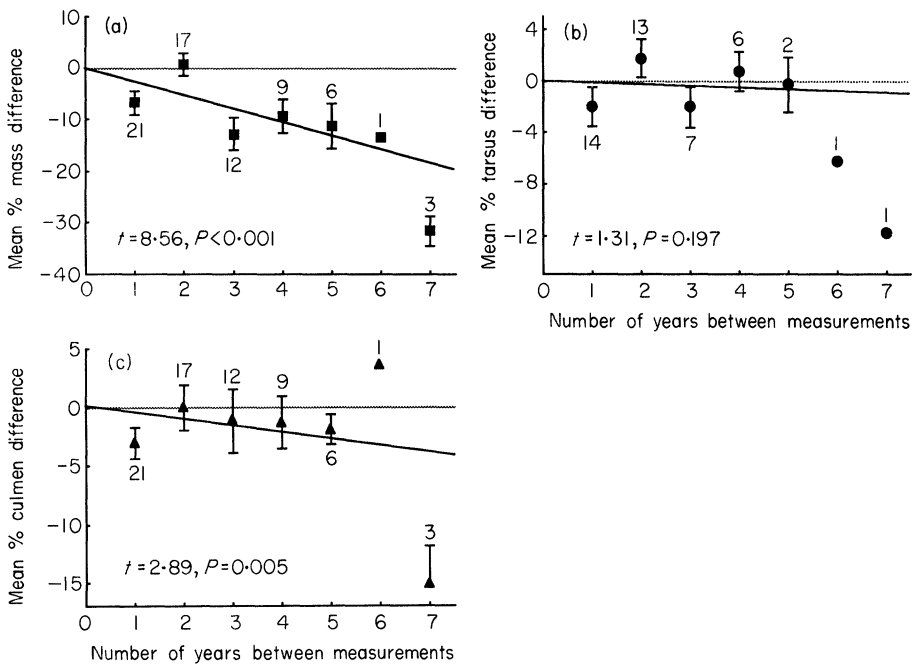


FIG. 2. Regression of percentage (a) body mass, (b) tarsus length and (c) culmen length difference in of goslings reared by individual adult females against number of years between measurement records. Individual gosling sizes linearly adjusted for differences due to hatch date, brood size and natal-year weather prior to calculation of differences. Statistics reported for analysis of arcsine-transformed percentages. Sample sizes differ for tarsus since tarsus was not measured in all years included in this analysis.

TABLE 2. Partial correlation of size of goslings reared by individual females with adult female age and year

(a) Partial correlation of gosling size with year controlling for age of adult female	
Body mass	-0.585 (<0.001)
Tarsus length	-0.353 (<0.001)
Culmen length	-0.241 (0.002)
(b) Partial correlation of gosling size with adult female age controlling for year	
Body mass	0.100 (0.199)
Tarsus length	0.100 (0.199)
Culmen length	0.099 (0.212)

Sample restricted to adult females age >4 . $n = 215$ for all measurements.

Effect on adult size

Analysis of 681 adult female lesser snow geese from the 1973–86 cohorts showed that decline in gosling size has caused a significant decline in adult body mass and structural size (Table 3; Fig. 3). To further illustrate the duration and magnitude of the decline, we include incomplete data from the 1969–72 cohorts in the figure. Over this complete range of data, adult body size, tarsus and culmen length declined by approximately 13%, 6% and 4%, respectively. (We report the percentage change for univariate structural measurements rather than PC1 as differences in principal components values cannot be properly expressed as proportions). Both adult body mass and structural size were significantly smaller with later relative hatch date during their hatch year. This reflects lack of complete compensatory growth of slower growing late hatching goslings (Cooch *et al.* 1990). Because the adult sample is comprised of a non-random subset of brood sizes (Cooch *et al.* 1990), brood size was not included in the analysis.

There was a significant decline in adult size, and a marginally significant decline in adult body mass ($P < 0.1$), with later absolute chronological hatch date, suggesting that annual differences in timing of breeding may significantly influence growth rates in this species. Adult age (in years) at the time of measurement did not explain a significant proportion of variation in adult structural size (entered as either a linear or a categorical variable), and was marginally significant for adult body mass ($P < 0.1$). Both structural size and body mass were significantly lower for birds that hatched in years with cool, wet weather.

DISCUSSION

This study documents an 18-year decline in the size of female lesser snow geese hatched and breeding at La Pérouse Bay, Manitoba. Body mass declined by 15%, while skeletal measures were 2–6% smaller. When data were available (1976–85),

TABLE 3. Multiple regression of adult size in lesser snow geese. (1973–86 cohorts)

Measurement	Term	<i>F</i>	<i>P</i>	Sign
Structural size	Hatch date ^r	17.14	<<0.001	–
	Hatch date ^m	6.30	0.012	–
	Age	2.98	0.085	+
	Weather	12.04	<0.001	+
	Cohort	19.69	<<0.001	–
	Model	18.39	<<0.001	R ² = 0.12
	Body mass	Hatch date ^r	24.39	<<0.001
Hatch date ^m		3.02	0.083	–
Age		1.67	0.197	+
Weather		4.42	0.036	+
Cohort		79.73	<<0.001	–
Model		33.74	<<0.001	R ² = 0.20

F-statistics calculated using partial (Type III) SS (SAS Institute, 1985). Hatch date^r = relative hatch date within season (*n* days ± annual mean within a season). Hatch date^m = annual mean hatch date (1 May = day 1). Sample size = 681 for all analyses. All interaction terms were not significant, and are not included in the table.

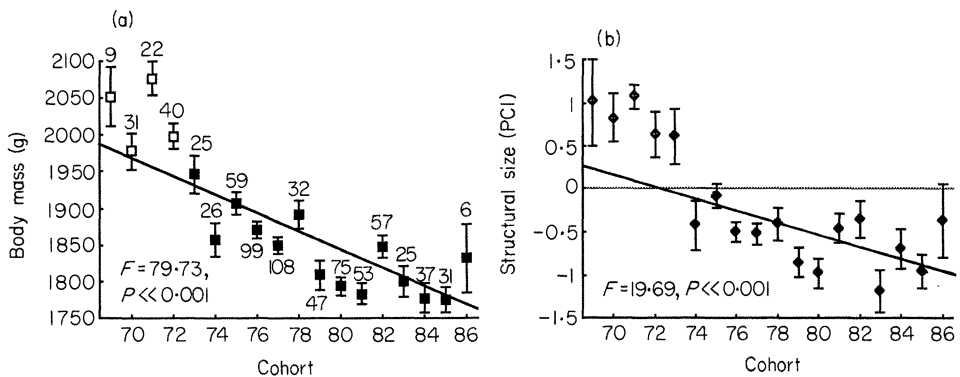


FIG. 3. Regression of (a) adult female body mass and (b) structural size (first principal component of culmen, head and tarsus length) against year. Annual means calculated as least-square estimates after adjusting size for hatch date, age and natal-year weather (see Methods). Mean values plotted with standard error of the mean and sample size. Data for 1969–72 cohorts included in figure (indicated by open symbols), but not in analyses presented in text or on figure.

the decline in size of annual cohorts was related to slower growth rates of goslings, at least during the first 20–40 days of life, in more recent years. A decline in the size of offspring of individual females was detected, suggesting an environmental, rather than genetic (or selectional) basis for the change. This result assumes no systematic change in the male genetic contribution (but see discussion below). Gosling growth rates were also slower in delayed seasons (late mean hatch date), and in seasons with cold, wet weather. Neither of these factors varied systematically during the study,

however. The slower growth in delayed seasons is in apparent agreement with F.G. Cooch, Stirrett & Boyer (1960) who showed that mean weights of immature snow geese harvested by hunters during the autumn migration was significantly lower in years with delayed breeding.

We have previously shown an environmental basis for changes in gosling growth rate within season relative to the timing of hatch and brood size (Cooch *et al.*, in press). We attribute the decline in size of breeding females to a long-term environmental change affecting gosling growth at the breeding colony.

Effect of mate change

There is approximately a 17% probability of mate change between any two breeding seasons (C.M. Francis, M. Richards, R.F. Rockwell & F. Cooke, unpublished), and the assumption of no mate change for adult females in this sample is unlikely to be completely supported. Males are believed to be chosen by the female on the wintering grounds (Cooke & Davies 1983), and are almost always from colonies other than La Pérouse Bay (Cooke, MacInnes & Prevett 1975). For mate change to cause the decline in size of goslings reared by individual females, the new males would have to be of systematically smaller body size. Because the size of the female does not change following mate change, the preference of the female for males of a specific size is also unlikely to change. Thus, we would predict that new males are not likely to be systematically smaller. Although we had insufficient data to restrict the preceding analyses to only those females who either had the same mate for all records, or for which we had measurements of different males for an individual female (which would allow us to statistically control for change in size of the male), we therefore feel it is very unlikely that mate change caused the decline in growth rates of goslings of individual females. Even if females choose a new mate randomly with respect to size of the male, this would tend only to increase genetic and phenotypic variation between broods, and decrease the probability of rejecting the null hypothesis that there are no significant inter-brood differences in gosling size within adult female.

Possible mechanisms

Intra-seasonal growth rates of young of several species of arctic nesting geese have been shown to be sensitive to differences in the quality or quantity of food (Cooch *et al.*, in press; Sedinger & Flint, in press; K. Larsson & P. Forslund, unpublished). Annual variation in food availability, either in terms of annual differences in foraging locations or productivity of primary food plants, might be predicted to cause correlated annual variation in gosling growth rates. The colony at La Pérouse Bay has increased significantly in size over time, resulting in increased numbers of geese utilizing the available resources, both prior to breeding, and during the post-breeding period (Cooch *et al.*, in press). Such a systematic increase in grazing pressure suggests that the decline in body size of goslings may be the result of a progressive decline in per capita food availability. Such a causal relationship between changes in intraspecific competition for food and annual variation in growth rates has previously been demonstrated in the herring gull (*Larus argentatus* Pontoppidan; Coulson, Duncan & Thomas 1982). However, lesser snow geese have a synergistic relationship with

their principal forage plants (Jefferies 1988). In controlled grazing experiments, grazing geese return sufficient fecal nitrogen to the system to sustain primary above-ground production and nitrogen content of the principal food plants (Cargill & Jefferies 1984; Bazley 1984; Hik & Jefferies 1990). Although the capacity of the vegetation to show compensatory growth following grazing declines over the course of the season (Bazley 1984; Hik & Jefferies 1990), possibly contributing to the seasonal decline in gosling growth rates, there is apparently little evidence of a significant long-term decline in the capacity of the forage plants to sustain the grazing levels experienced at the colony (R.L. Jefferies, pers. comm.). However, there has been a measurable decrease in the amount of available food on the traditional grazing flats at La Pérouse Bay, and a decrease in overall food abundance over the past several years. The most plausible mechanism appears to be the destructive effects of pre-season grubbing by the geese. Such grubbing destroys the below-ground biomass of the forage plants, and may ultimately reduce the available above-ground forage during brood rearing (R.L. Jefferies, pers. comm.). The cumulative long-term effects of pre-season grubbing and grazing during the brood rearing period on the abundance of the principal food plants is currently under investigation.

Alternatively, there may be increasing utilization of sub-optimal food sources as the numbers of geese breeding at the colony increases. Use of secondary food plants has been shown to significantly reduce growth rates in other goose species (Sedinger & Flint, in press). In addition, the increased numbers of geese at the colony may increase the proportion of time spent in agonistic encounters between families, and decrease the overall time spent foraging. Both scenarios would be predicted to lead to a long-term decrease in growth rates, and are currently under investigation.

Life history consequences

Body size variation in birds can significantly influence both fecundity (Ankney & MacInnes 1978; Murphy 1986; Richner, Schneyer & Stirnimann 1989) and survival (Perrins, Harris & Britton 1973; Harris & Rothery 1985; Hepp *et al.* 1986; Owen & Black 1989; Conroy *et al.* 1990).

Fecundity

There has been a significant long-term decline in annual mean clutch size at La Pérouse Bay, correlated with increases in both the local and continental population sizes (Cooch *et al.* 1989). This decline was attributed to a decreased potential for geese to acquire nutrient reserves, presumably resulting from increased competition for available food during the spring migration. However, the long-term decline in adult body size suggests an alternative explanation. Alisauskas (1988) has suggested that the structural size of adult female lesser snow geese ultimately limits the quantity of nutrient reserves an individual can acquire during the pre-breeding period. The size of the nutrient reserves acquired by adult females during the spring migration has been shown to limit clutch size in arctic nesting geese (Ankney & MacInnes 1978). Therefore, a decrease in structural size over time might be predicted to cause a decrease in the size of the nutrient reserves carried to the breeding site by an individual female, with a concomitant decrease in clutch size.

There are two pieces of evidence that suggest that this hypothesis alone may not be valid. Davies, Rockwell & Cooke (1988) showed that body size and clutch size

were independent in an analysis using a subset of the data pooled over years (but see Alisauskas & Ankney 1990; Cooke, Davies & Rockwell 1990). Further, Cooch *et al.* (1989) demonstrated that the clutch size of individual birds also declined significantly over time. As the structural size of an individual adult female is constant beyond the age of 1 year (Davies, Rockwell & Cooke 1988), this suggests that the long-term decline in clutch size cannot be due to the long-term decline in adult size alone. However, neither Davies, Rockwell & Cooke (1988) nor Cooch *et al.* (1989) analysed individual variation *within* cohort. The highly significant cohort effect may have confounded some of the pertinent analyses, and the ultimate relationship between body size and clutch size in this species remains under investigation.

Survival

Early hatching goslings are recruited into the breeding population at a significantly greater rate than late hatching goslings (Cooke, Findlay & Rockwell 1984), presumably, in part, because of their greater growth rates (Cooch *et al.*, in press). While the possible correlation between seasonal differences in gosling growth rate and survival to breeding age is currently being assessed, Owen & Black (1989) demonstrated a highly significant positive relationship between body size and survival in first-year barnacle geese (*Branta leucopsis*, Bechstein). There is some evidence that the long-term decline in gosling size may have consequences on first-year survival, which has declined significantly over the course of the study (C.M. Francis, M. Richards, R.F. Rockwell & F. Cooke, unpublished).

We have previously demonstrated that seasonal differences in gosling growth rates are significantly affected by timing of hatch and brood size (Cooch *et al.*, in press). In this study, we have shown that both post-hatch weather and long-term changes at the breeding site have also significantly affected gosling growth rates and subsequent adult size. The possible consequences of body size variation in lesser snow geese on both fecundity and survival, and the significant effects of various environmental factors on variation in body size in this species, suggests that it is prudent for evolutionary biologists to carefully consider the degree to which fitness differences among individuals relates to the environmental component of the phenotype, and not solely the genetic component (*sensu* van Noordwijk, van Balen & Scharloo 1988).

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