Body size variation in barnacle goose colonies: Evidence for local saturation of habitats

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Adult body size of Svalbard-breeding barnacle geese *Branta leucopsis* is significantly influenced by foraging conditions experienced at an early age in brood-rearing areas. Adult body size declined significantly between 1975 and 1993, the maximum decline being –0.4 mm/yr. Decline in body size varied among colonies and brood rearing regions in Svalbard, with the sharpest decline occurring in the Kongsfjorden population which had rapidly increased in number ($\lambda = 1.12$) since 1977. Body size was closely correlated with the age of the colonies (i.e. duration since the first nests), which ranged between 6 and 48 years. We believe that variation in body size evidenced over time and among areas was related to relative density of geese and length of time that they had exploited local food resources.

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Introduction

The size of an individual can have profound implications on a range of life history traits. For example, body size has been implicated in the amount of food required for daily maintenance and the competitive ability necessary to obtain the food. Structural size has also been linked with the propensity with which animals survive, find mates and reproduce (see case studies in Clutton-Brock 1988a; Newton 1989; Black 1996).

Body size is a critical feature for geese that strive to avoid aerial attacks from predators and attempt to migrate long distances efficiently. Geese must also be able to compete with numerous flock members for forage, mates and nest sites, in addition to avoid ground dwelling predators. Whereas small body sizes may be useful in some situations, larger body size may be adaptive in others (Black et al. 1996; Choudhury et al. 1996). Several recent studies of arctic geese have found that the amount and quality of food that a gosling obtains in early life (<8 weeks) affects adult body size (Cooch et al. 1991a; Sedinger & Flint 1991; Larsson & Forslund 1991, 1992; Sedinger et al. 1995; Loonen et al. 1997, 1998 (this volume). The argument from the lesser snow goose *Anser caerulescens caerulescens* study is that several traits, including body size, have changed over time due to the deleterious effect that overgrazing has had on the vegetation that the geese require (Cooch et al. 1991b; Cooke et al. 1995). We have yet to detect a decline in vegetation quality in our study but have begun to see signs of increased competition for a limited amount of food (Prop et al. 1984; Owen & Black 1989, 1991; Loonen 1997). In either case, goslings with limited food and suboptimal growth become small adults, while goslings reared with sufficient food become larger adults. Similar phenomena are suspected in a range of animals (Clutton-Brock 1988b), but evidence is fairly limited in vertebrates, for example final body size of young deer varies according to foraging and suckling performance (Klein 1970; Clutton-Brock et al. 1982; Albon et al. 1987).

Adult body size variation within goose populations has been recorded in several recent studies. However, in most cases it has been difficult to account for the effects of temporal *and* spatial variation (for example over time: Cooch et al. 1991a, b; Larsson & Forslund 1991, 1992; Loonen et al. 1997, and in different locations or of different origins: Owen & Black 1989; Aubin et al. 1993). Studies that attribute the change in final body size to time-related events have been unable to check whether the phenomenon is common across sites, and those that attribute variation to differences in sites have not been able to rule out temporal effects. It is probable, however, that both temporal and spatial variation in growth on the breeding grounds (which influences final adult body size) will have a nontrivial impact on population dynamics, for example mate choice and differential reproductive success: sensu Cooch et al. (1993).

In this paper we examine data from six barnacle goose *Branta leucopsis* colonies on Svalbard with respect to temporal *and* spatial scale. We argue that differences in adult body size are linked to the length of time that an increasing number of geese have put increasing pressure on the food resources, i.e. density limitation on goose food.

Methods and procedures

The population

In the 1940s, the barnacle goose population in Svalbard declined to only 300 individuals. The population responded to a series of conservation and management initiatives in the wintering and breeding grounds with an increase of 7.8% per year since 1960 (Pettifor et al. 1998, this volume). In the 1990s, the population reached unprecedented levels (23,000 individuals in 1996), and the geese expanded their range in the wintering haunts on the Solway Firth, in northern Britain, and on staging areas in Norway (Owen et al. 1987; Black et al. 1991; Prop et al. 1998). The number of colonies in Svalbard has also increased to more than 35, mainly on the western coast of Spitsbergen between 77° and 80°N (Prestrud et al. 1989). The population is probably larger now than in the past (Black 1998a). As a result of the increase in numbers, we have recorded changes in several demographic parameters, including an increased age of first breeding, a large increase in the non-breeder contingent, a decrease in many reproductive parameters, and an increase in gosling and adult mortality during autumn migration (Prop et al. 1984; Owen & Black 1989, 1991; Pettifor et al. 1998, this volume). We believe that many of these changes are directly related to a decline in food availability, either because of vegetation depletion due to intensive goose grazing (sensu Williams et al. 1993) or because of reduced access to food due to increased competition (Prop et al. 1984; Owen & Black 1989).

Study sites

Thirteen expeditions to Svalbard were made since 1973 in order to capture and measure the geese prior to fitting individually-engraved, plastic leg rings. Seven regions with major colonies were revisited in different years and two were visited regularly, Nordenskiöldkysten between 1977 and 1995 and Kongsfjorden from 1989 to 1995 (Fig. 1). We assume that colony age, as calculated from the discovery date, provides a useful variable for linking bird numbers to final body size and to the quantity of food available to goslings. Although these sites may have been used by small numbers of geese centuries before their discovery, some of the discovery dates indicate a relative colony age that is closely correlated with bird density in each area (Prestrud et al. 1989, see below).

Nordenskiöldkysten was split into three stretches of coastline, each with its own island colonies: St. Hansholmane in the north, Diabasøya in the middle, and Reiniusøyane in the south (Owen et al. 1978). The vast majority of geese remained loyal to one of these island colonies over a five-year period; only 5 of 120 pairs changed sites (Prop et al. 1984, also see Black 1998b). The northern Nordenskiöldkysten colony (St. Hansholmane) was established in 1963, the middle colony (Diabasøy) in 1968, and the southern colony (Reiniusøyane) in about 1975. The first nest in the (Kongsfjorden colony was established in 1980, although a non-breeding flock used the area since at least 1977 (P. Prestrud, pers. comm).

Measurements

Measurements were made during banding expeditions on Svalbard during the annual adult feather moult. Although development of body mass in

Fig. 1. Map showing the study colonies and brood rearing areas on Spitsbergen, Svalbard.

goslings is known to be more sensitive to variations in early growth conditions than skeletal characters (see for example Cooch et al. 1991b, 1996), adult body mass measured at ringing is much affected by breeding status (Owen & Ogilvie 1979; Choudhury et al. 1992). Many ringing campaigns were significantly biased with respect to breeding status. Thus, we restricted our analyses to head and tarsus length ('tarsus bone' – Dzubin & Cooch 1992; both characters measured to the nearest 0.1 mm). We used the mean of measurements made for each individual in the sample in different years to minimise effects of measurement error. This is valid since barnacle geese do not grow significantly after the first year (Owen & Ogilvie 1979).

Statistical approach

We used multivariate analysis of variance (MANCOVA) approaches to test for overall differences among cohorts in structural size (head and tarsus length). We controlled for variation due to sexual size dimorphism by including sex as classification factor in all analyses (sensu Cooch et al. 1996). While MANCOVA is robust for estimating the significance of overall differences in size, previous studies of body size variation in this and other goose species have shown that different characters may show different responses to changes in growth conditions (e.g., Larsson & Forslund 1991; Cooch et al. 1991a, b, 1996). Thus, we also analysed variation in tarsus and head length separately, using univariate procedures.

Since the colonies were initiated at different years and their rate of expansion varied, we expected spatial differences that corresponded to the history of these events (sensu Cooch et al. 1993). We examined this by comparing the pattern of body size variation in two colonies over the same study period. We also compared size data for all colonies, adjusted for colony age (see below).

Assigning natal colony

The absolute assignment of adults to a specific natal colony is only possible for birds ringed as young. Using a very large sample of ringed goslings, Cooke et al. (1975) showed that lesser snow geese have a strong female philopatry to the natal colony, whereas males do not. In this population of barnacle geese both sexes are highly philopatric, although males changed sites more often than females (Black 1998b, this volume; Loonen et al. 1998, this volume). Birds encountered at more than one colony (<5% of the total sample) were assigned to the colony at which they were measured for the first time.

Assigning age (Cohort)

Birth-year of birds ringed as goslings and yearlings (and therefore birth-cohort) was determined precisely. Birds marked as adults were assigned a minimum age of two years (and thus a birth-cohort of year-2). The earliest age of first-breeding in barnacle geese is two years. However, there are some potential problems with this approach. The probability of not capturing a bird during ringing is proportional to the proportion of the total population sampled. Some birds will generally be missed over one or more ringing occasions. For such birds, the minimum age estimate of two years will be negatively biased with respect to their true ages. This is potentially of concern in growing populations, where a constant ringing effort means a decline in sampling fraction over time (i.e., increasing bias in assigned age). The Svalbard barnacle goose population grew significantly over the course of this study (Black 1998a). An increasingly negative bias in assigned ages will reduce the estimated slope of the relation between body size and cohort. In our data, only 34% of the adult sample is of known age (based on proportion of birds ringed as goslings or yearlings). Thus, the results of some of our analyses may be subject to slightly increased Type I error (at the $\alpha = 0.05$ level).

Analysis was restricted to two primary colonies for which adequate data existed to examine temporal trends in body size. These two colonies comprised 83% of the total sample (2,826 of 3,406 total individuals). Sample sizes for some cohort-colony combinations were very small. To minimise the effects of these sparse cells in factorial analyses, we eliminated data from samples with fewer than ten individuals. For analyses where cohort was included as a linear covariate, all available data were used.

Results

Within-colony variation (temporal scale)

When the sexes were pooled, there was a highly significant long-term decline in structural size for both the Nordenskiöldkysten (MANCOVA $F_{2,2178} = 7.10$, $P < 0.001$) and Kongsfjorden colonies (MANCOVA $F_{2,634} = 18.82$, $P < 0.001$) (see Fig. 2 for ANCOVA results on head and tarsus).

There was no overall difference in slopes between males and females for both the Nordenskiöldkysten (MANCOVA $F_{2,2177} = 2.02$, $P = 0.133$) and Kongsfjorden colonies (MANCOVA $F_{2,2633} = 1.07$, $P = 0.345$). However, when head and tarsus were considered independently, there was some indication that the decline in head length in Nordenskiöldkysten females was more rapid

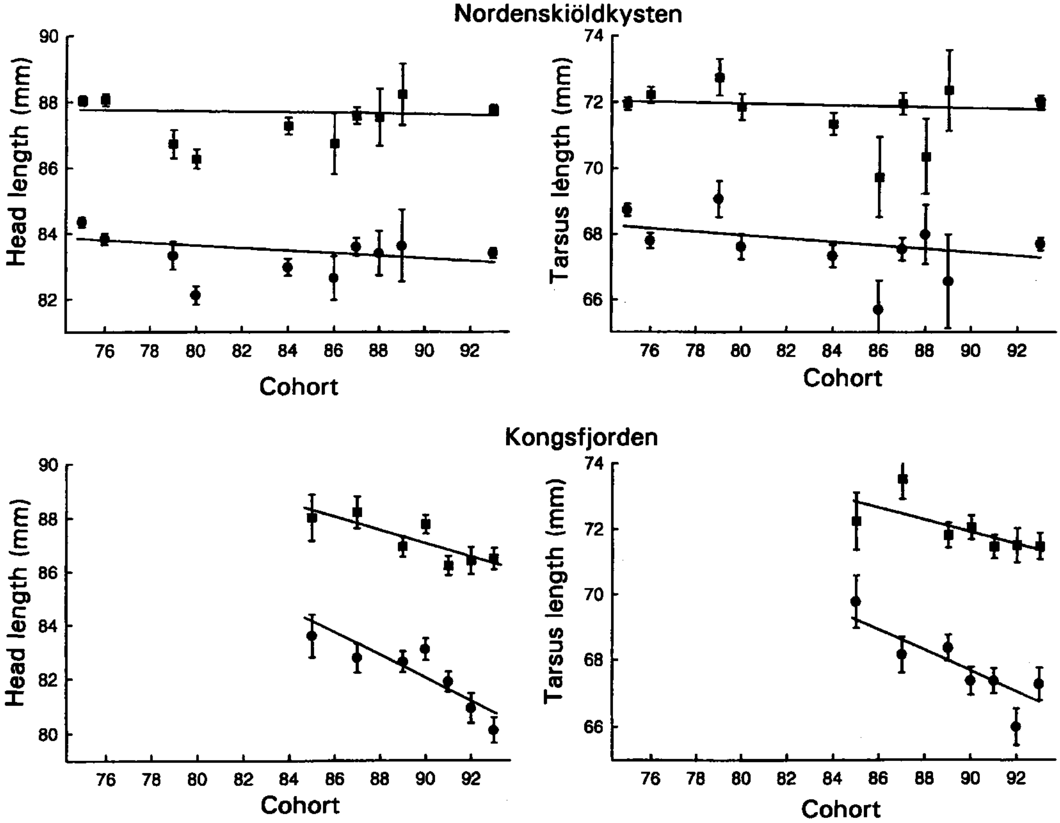

Fig. 2. Variation in head and tarsus measures over several cohorts for birds living in two localities. There was a highly significant long-term decline in head for both the Nordenskiöldkysten (ANCOVA $F_{1,2179} = 13.76$, $P < 0.001$) and Kongsfjorden colonies (ANCOVA $F_{1,635} = 34.92$, $P < 0.001$) and in tarsus for both the Nordenskiöldkysten (ANCOVA $F_{1,2179} = 6.83$, $P = 0.009$) and Kongsfjorden colonies (ANCOVA $F_{1,635} = 18.42$, $P < 0.001$). Males (squares), females (dots).

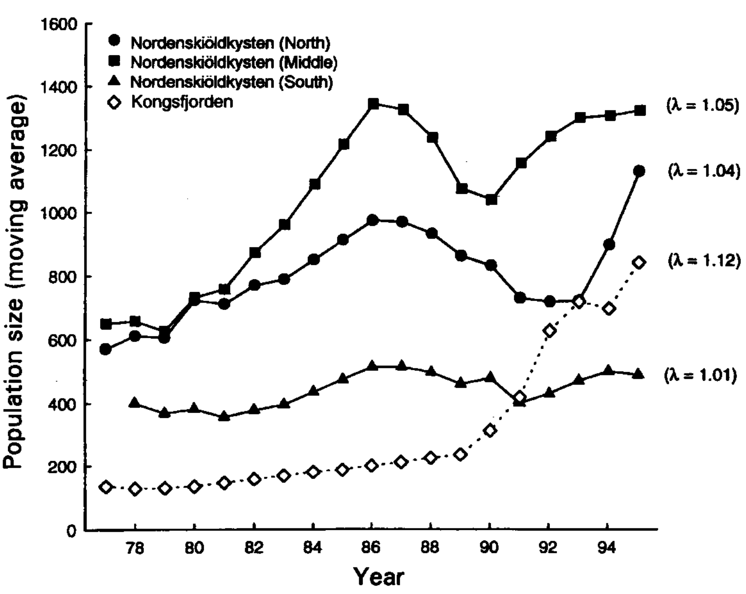

Fig. 3. Number of geese (including breeders and non-breeders) and population growth (given as λ values) for three Nordenskiöldkysten sub-colonies and the Kongsfjorden area. We calculated values for missing years using a simple linear interpolation (excluding the spurious value for the south in 1977) and calculated lambda (λ) with the following formula: $\ln(\lambda) = (\ln(NT) - \ln(N1))/(T - 1)$, where ln is log number, N is population size, T is range of years. The northern Nordenskiöldkysten colony (St. Hansholmane) was established in 1963, the middle colony (Diabasøya) in 1968 and the southern colony (Reiniusøyane) in about 1975. The first nest in the Kongsfjorden colony was established in 1980, although a non-breeding flock used the area since at least 1977. (Black 1998, this volume).

than in males (ANCOVA $F_{1,2178} = 3.68$, $P = 0.055$).

Between colony variation (spatial scale)

We compared the relative magnitude of the decline in structural size of birds from different areas in several ways. The establishing dates, i.e. the age of the colonies, and the rate of population growth differed slightly for the Nordenskiöldkysten colonies (Fig. 3). We predicted that any changes in body size over time should be related to these colony age and growth differences. Pooling the sexes and using an ordered linear contrast, we tested whether or not the rate of the decline within three sub-colonies on Nordenskiöldkysten corresponded to their relative ages. Although tarsus was clearly nearer to significance than head length, the overall difference between sub-colonies in the relationship between cohort and sex was not significant (MANCOVA $F_{6,4346} = 1.160$, $P = 0.227$; for tarsus alone ($F_{3,2174} = 2.25$, $P = 0.081$) and for head alone ($F_{3,2714} = 1.29$, $P = 0.275$)). With increasing colony age, there was a significant increase in the rate of the decline in structural size ($F_{4,3196} = 8.98$, $P < 0.001$).

A comparison of slopes indicated the change in body sizes of the three sub-colonies without pooling the sexes (Fig. 4). The comparison showed that body size became increasingly smaller from south (young colony with a small rate of population growth λ) to north (older colony with a larger λ) (Table 1). For the southern and middle colonies, the slopes themselves were not significant, but, based on a series of paired comparisons, there was a trend from south to north (Table 1). This was the case for both sexes regarding head length measures and for females regarding tarsus measurements.

The age of the colony is only one possible factor that contributes to the spatial differences in body size. Colonies may be of similar age, but because of differences in habitat or number of birds among the colonies, the relative food abundance may differ significantly. This is clearly seen by comparing data from the 'south' and 'middle' sub-colonies at Nordenskiöldkysten with data from the Kongsfjorden colony, over the same range of calendar years (cohorts 1985–1993). Pooling the sexes revealed a highly significant difference between the two regions in the pattern

Table 1. Comparison of the change in body size mm/yr (the slopes) between the three Nordenskiöldkysten colonies. The upper panel indicates the slopes and SE and the lower panel provides results of paired ANCOVA comparisons. Asterisks indicates slopes that are significant; $P < 0.05$.

Colony	Head length		Tarsus length	
	male	female	male	female
South: Reiniusøyane	0.00004 (0.031)	0.059 (0.032)	−0.28 (0.042)	0.043 (0.043)
Middle: Diabasøya	−0.003 (0.013)	−0.012 (0.014)	0.014 (0.017)	0.007 (0.018)
North: St. Hansholmane	−0.166* (0.052)	−0.389* (0.060)	−0.002 (0.068)	−0.267* (0.078)
Paired comparisons				
South vs middle	$F_{1,1263} = 0.01$, $P = 0.903$	$F_{1,1255} = 4.41$, $P = 0.036$	$F_{1,1088} = 0.79$, $P = 0.374$	$F_{1,1085} = 0.63$, $P = 0.428$
South vs north	$F_{1,1263} = 12.58$, $P < 0.001$	$F_{1,1255} = 41.66$, $P < 0.001$	$F_{1,1088} = 0.11$, $P = 0.743$	$F_{1,1085} = 14.63$, $P < 0.001$
Middle vs north	$F_{1,1263} = 23.15$, $P < 0.001$	$F_{1,1255} = 43.21$, $P < 0.001$	$F_{1,1088} = 0.06$, $P = 0.814$	$F_{1,1085} = 14.53$, $P < 0.428$
Overall	$F_{1,1263} = 12.07$, $P < 0.001$	$F_{1,1255} = 27.26$, $P < 0.001$	$F_{1,1088} = 0.41$, $P = 0.666$	$F_{1,1085} = 7.95$, $P < 0.001$

of variation in body size over cohorts ($F_{2,1443} = 16.80$, $P < 0.001$); within Nordenskiöldkysten, over this range of cohorts, there was no significant change in structural size over time. However, at the Kongsfjorden colony, body size declined more markedly over time (Fig. 2).

Cooch et al. (1991a,b, 1996) showed a significant variation among lesser snow goose skeletal characters in response to variation in growth conditions. They concluded that culmen length, which corresponds to head length, showed greater developmental plasticity than did tarsus length. If the same general relationship holds for barnacle geese, we predict that the pattern of variation in head length among sub-colonies should be greater than that observed for tarsus length. ANCOVA, comparing the rate of decline in each character over cohort, supported this prediction. There was highly significant variation in head length among sub-colonies in Nordenskiöldkysten in the rate of decline ($F_{2,1944} = 17.69$, $P < 0.001$), while there was no detectable difference in tarsus length among sub-colonies ($F_{2,1600} = 1.69$, $P = 0.184$).

The detection of this sub-colony variation indicates that it is worth controlling for differences in colony age when comparisons are being made in changes in body size. Direct comparisons among spatially distinct sub-groups according to calendar year of birth (cohort) may be difficult to interpret unless the age of the sub-groups, relative to age of the colony as a whole, is known.

As such, it may be possible to broadly contrast all colonies in our sample simultaneously by scaling cohort relative to the year of origin of the colony (Table 2) rather than scaling to the absolute colony year. For example, the Kongsfjorden colony and its associated brood rearing area near the village of Ny-Ålesund originated in 1980, based on discovery of the first nest (Fig. 1). Thus, we can scale cohorts relative to this date using the transform: relative cohort = calendar cohort − colony origin year. Adults from the 1990 cohort of the Kongsfjorden colony would thereby be rescaled to relative cohort 10. Upon application of this transformation to all colonies, we found a significant decline in structural size with increased colony age (Fig. 5). These over-all colony findings are consistent with the preceding comparison among sub-colonies at Nordenskiöldkysten (Fig. 4).

Table 2. Statistics for seven barnacle goose colonies on Svalbard. Measurements are given in mm. Values in parentheses are SE.

Colony	Latitude	First colony record	Female head length	Male head length	Female tarsus length	Male tarsus length	Sample sizes Male, Female
Isøyane and Dunøyane[1]	77,05°N	1938	82.00 (0.20)	86.53 (0.21)	65.51 (0.24)	70.43 (0.25)	193, 192
Nordenskiöldkysten[2]	77,50°N	1969	83.60 (0.07)	87.71 (0.08)	67.94 (0.10)	71.96 (0.10)	1090, 1092
Daudmannsodden[2]	78,12°N	1970	80.61 (0.46)	85.01 (0.45)	67.75 (0.57)	71.64 (0.67)	41, 37
Prins Karls Forland[2]	78,20°N	1963	80.01 (0.46)	82.51 (0.53)	66.28 (1.22)	71.34 (1.00)	12, 14
Sassendalen[3]	78,18°N	1963	83.41 (0.55)	88.44 (0.49)	67.81 (0.82)	72.87 (0.51)	21, 15
Gåsøyane, Gipsdalen[3]	78,27°N	1980	83.69 (0.79)	87.34 (0.45)	66.65 (0.68)	71.92 (0.58)	20, 19
Kongsfjorden, Ny-Ålesund[3]	78,55°N	1980	82.13 (0.17)	86.98 (0.17)	67.62 (0.17)	71.85 (0.18)	304, 334

[1] = *Papaver dahlianum* vegetation zone; [2] = *Dryas octopetala* vegetation zone; [3] = *Cassiope tetragona* vegetation zone.

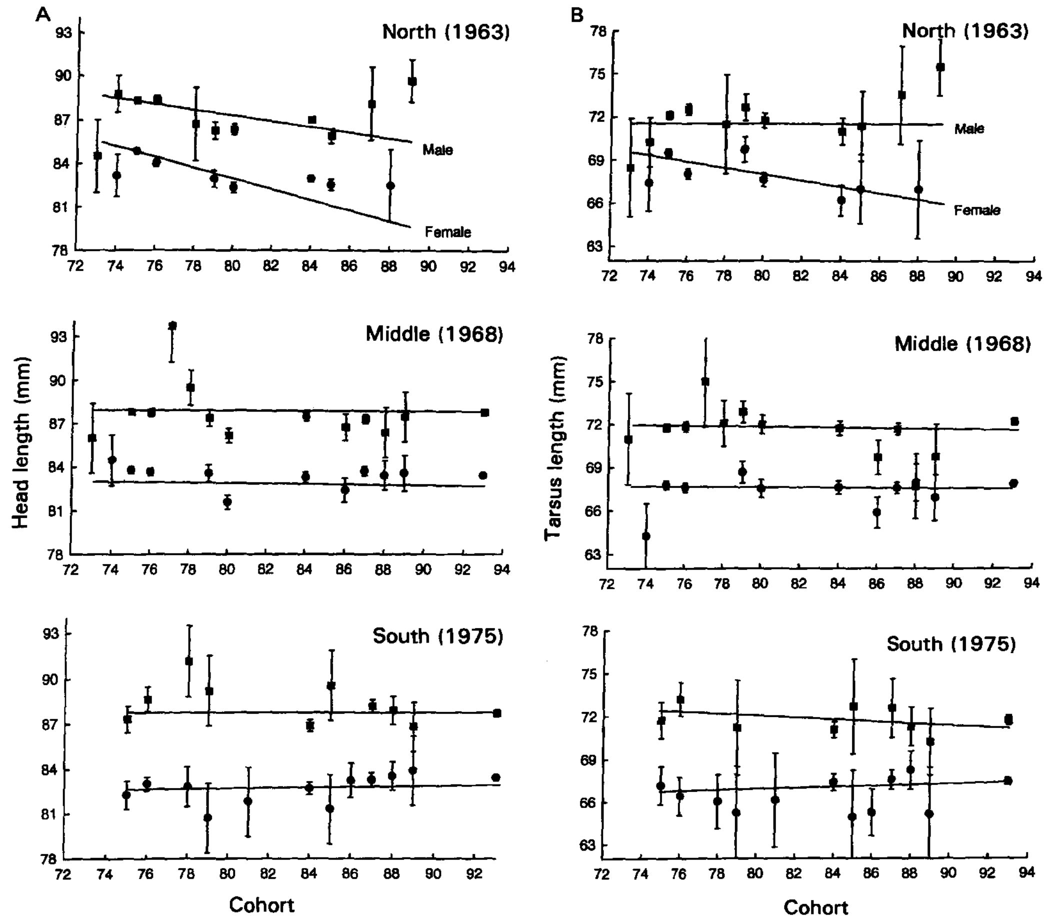

Fig. 4. Variation in A head and B tarsus length for three sub-colonies on Nordenskiöldkysten; males (squares), females (dots). Northern colony (a): Overall difference between the sexes was significant (MANCOVA $F_{2,650} = 4.48$, $P = 0.0.12$) so the data were not pooled. There was a significant linear change with cohort for head length (females: ANCOVA $F_{1,505} = 41.99$, $P < 0.0.001$; males: ANCOVA $F_{1,490} = 9.98$, $P = 0.0.002$) and for tarsus in females (females: ANCOVA $F_{1,79} = 11.70$, $P < 0.0.001$; but not in males: ANCOVA $F_{1,79} = 0.0009$, $P = 0.974$). Middle colony (b): Pooling over sexes, no significant linear change in size was detected across cohorts (overall size, MANCOVA $F_{2,1110} = 1.32$, $P = 0.268$; head length, ANCOVA $F_{2,1111} = 0.59$, $P = 0.441$; tarsus ANCOVA $F_{2,1111} = 0.74$, $P = 0.389$). Southern colony (c): Pooling over sexes, no significant linear change in size was detected across cohorts (MANCOVA $F_{2,411} = 1.11$, $P = 0.329$; head length, ANCOVA $F_{2,412} = 1.75$, $P = 0.187$; tarsus ANCOVA $F_{2,412} = 0.05$, $P > 0.5$).

Discussion

With the increase in the Svalbard barnacle goose population, from 3,200 in 1970 to 23,000 in 1996 (Black 1998a), far more geese have been harvesting the sparse arctic vegetation. Prop et al. (1984) gives evidence from Nordenskiöldkysten that food depletion during the breeding season has a limiting effect on reproduction. When the first geese through an area take most of the available food, the competition for the remaining food is intensified as the season progresses. Geese arriving at a patch that has already been visited by other geese have fewer items to choose from. In addition, the intake rate on previously grazed plants is much reduced (Prop & Loonen 1988). Plant depletion is greater when goose density increases.

On Nordenskiöldkysten numbers increased from 1,060 in 1975 to 3,146 in 1995 (Fig. 3), an

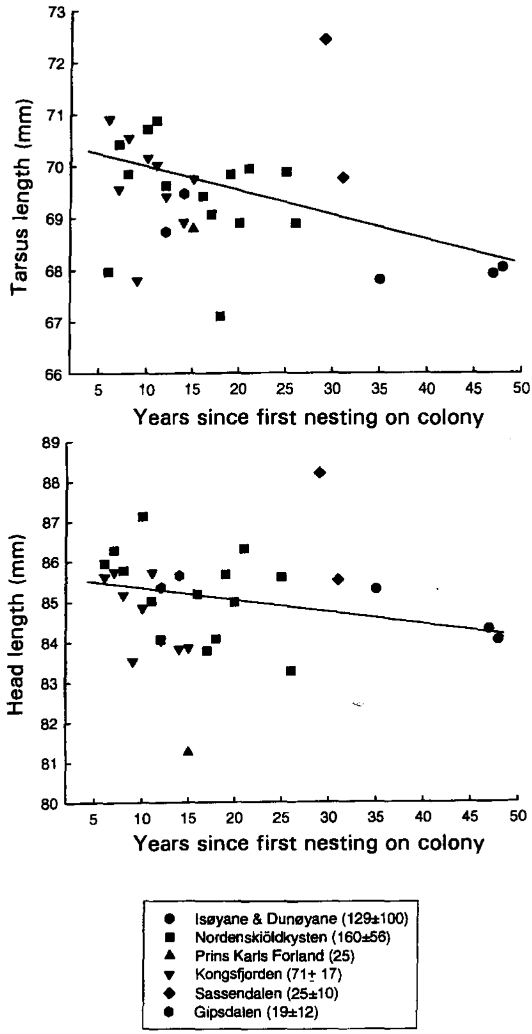

Fig. 5. Body size variation for six colonies of various ages. There was a highly significant decline in body size with colony age (overall MANCOVA $F_{2,3298} = 41.95$, $P < 0.001$); head length declined by about 0.03 mm/yr ($F_{1,3671} = 29.96$, $P < 0.001$), while tarsus declined by about 0.05 mm/yr ($F_{1,3301} = 83.27$, $P < 0.001$). The numbers in parentheses in the legend refer to mean sample size and SD.

increase of 4–5% per annum over the 20-year period in the northern and middle sectors. For the southern sector, numbers increased only 1% per annum. At the more recently colonised Kongsfjorden site, the number of birds increased at a much greater rate, from 135 birds in 1977 to 995 in 1995 (12% per annum) (see Loonen et al. 1998, this volume). The increase corresponds well with the hypothesis that body size reduction is related to the amount of food available per goose. Whereas body size has decreased substantially at Kongsfjorden, at Nordenskiöldkysten the decline is less steep and reflects numbers within sub-populations.

Body size variation over time and between areas may therefore be related to the relative density of geese that exploit local food resources. In the early years of colony expansion by lesser snow geese at La Pérouse Bay, the population increased by 7–11% per annum, whereas in recent years population growth has declined to <1% per year (Cooke et al. 1995). In that study, vegetation was degraded by overgrazing, and body sizes declined as the population increased towards the habitats' carrying capacity (Cooch et al. 1991b; Cooke et al. 1995). If the same situation is occurring in Svalbard, it would follow that Kongsfjorden is still in rapid expansion, the northern and middle areas of Nordenskiöldkysten are intermediate, and the southern area of Nordenskiöldkysten has already reached saturation. These trends correspond with variation in body size in that the most dramatic changes were seen at Kongsfjorden and north Nordenskiöldkysten, two areas with substantial population growth (Fig. 3). In contrast, body size variation in southern Nordenskiöldkysten is entirely flat (Fig. 4), perhaps because numbers there have not changed in recent years.

Habitat saturation appears to have been reached at the Kongsfjorden colony in 1992, when gosling growth was thereafter substantially reduced (Loonen et al. 1997, 1998, this volume). The correlation between colony age and body size (Fig. 4) may, therefore, reflect the location of colony with respect to the limitation on the vegetation or overpopulation of an area.

It is worth considering why body sizes from middle Nordenskiöldkysten have not declined as much as those from the northern area, even though population growth in these areas has been about the same. Fig. 3 clearly shows that the north colony was at a plateau for a greater number of years than the middle colony. Specifically, from 1985 on, numbers in the north seemed rather stable, and between 25–35% more than the middle area. Perhaps this greater period of 'sustained grazing' pressure explains why body size has declined only in the north.

We favour the habitat saturation hypothesis rather than the alternative—an increasing mortality selection against large adults—because Cooke et al. (1995), after an extensive analysis, reported that adult body size did not influence survival. The type and phenology of the plants are variables that may effect body size differences between colonies and which are related to the timing of the spring thaw (Prop & de Vries 1993). If geographic variation in vegetation phenology influences body size variation, we might expect larger-sized geese in warmer areas and vise versa.

Evidence for the long-term decline in structural size is manifest primarily by a decline in the head (culmen) rather than in the tarsus. Loonen et al. (1997) showed that whereas tarsus is already close to full size on the 35th day, head size has only reached 90% of its full size. Considering that barnacle geese harvest their diet with their bills at rates of more than 200 pecks per min, head size may be more sensitive to environmental conditions. Individuals adjust their peck rate according to the type, height and tenderness of the food. Across goose species, peck rate is closely matched to head (and bill) size; small bills correlate with quicker rates of harvesting (Owen 1980).

A corresponding change has perhaps not been detected in tarsus length because tarsus length sets an upper limit on allowable body size and is thus conserved. If tarsus size, which also controls terrestrial locomotion, becomes too small, the maximum size body that a goose can efficiently move may be smaller. Alternatively, arctic foxes *Alopex lagopus* may select slower geese with smaller legs. The fox capture-strategy is to dart into and scatter an unsuspecting flock of families and to take the slowest goslings as they attempt to run to the nearest body of water (see for example Prop et al. 1984).

Future investigations should include an assessment of the impact that a reduction in body size may have on population dynamics. Body size is positively correlated with various fitness components in barnacle geese (Larsson & Forslund 1992; Choudhury et al. 1996), black brant (Sedinger et al. 1995), and Canada geese *Branta canadensis* (Lessells 1982), whereas the evidence for lesser and greater snow geese is less clear (Ankney & MacInnes 1978; Alisauskas & Ankney 1990; Davies et al. 1988; Cooch et al. 1992; Choiniere & Gauthier 1995). Body size itself may influence annual reproductive variables in some species. However, the conditions which lead to reduced adult size will probably affect all species because these conditions impact gosling growth and survival (Cooch et al. 1991a; Owen & Black 1989), for example through increased competition for food or a degraded habitat. The phenomenon of declining structural size may well be ubiquitous among goose populations whose numbers have risen to unprecedented levels. This applies to the Swedish population of barnacle geese (Larsson & Forslund 1991, 1992; Larsson 1993), to lesser snow geese (Cooch et al. 1991 b), and to greater snow geese *Anser caerulescens atlantica* (Gauthier & Reed pers. comm.).

Examining both males and females separately, Choudhury et al. (1996) found that larger-sized barnacle geese had a higher probability of breeding successfully in any particular year and producing a greater number of offspring than smaller birds. However, in species like geese, whose pair bond members maintain proximity throughout the day and often for life, reproductive success of an individual will be influenced by the investment or actions of the partner (Black & Owen 1995). In barnacle and lesser snow geese, both males and females appear to maximise their breeding performance with similar-sized partners (Choudhury et al. 1996). The larger the size-mismatch between mates, the lower the breeding performance. This suggests that reproductive success of a pair may not only be determined by their qualities as individuals, but also by their degree of compatibility or complementarity. Despite the consequences of this size disparity, barnacle geese choose mates in a random fashion with respect to body size (Choudhury et al. 1992). Hence, any change in population recruitment due to a reduction in body size will be influenced by the body size of both partners (and compatibility in their sizes) which may come from different cohorts with different body sizes.

The decline in availability and quality of vegetation, which drives body size variation in geese, has begun to impact sex ratio in gosling cohorts. More females are surviving since the larger male goslings require more food during early life (Cooch et al. 1996, 1997). Whereas male body size was apparently more sensitive to environmental change in snow geese, it was the female body size in our study that declined proportionately faster than males (Figs. 2 and 4). Perhaps male body size declines more than females only when feeding conditions are dire, as was the case in the lesser snow goose study.

It remains to be seen whether geese of the genus *Branta* will degrade arctic vegetation to the same degree as has been done by snow geese. Habitat degradation in areas used by snow geese has been caused by the geese feeding on underground plant parts, which kills the plant (Cooke et al. 1995). This behaviour is less common in *Branta*. Perhaps goose-plant interactions are more stable with *Branta*; two of four populations that we report had stable body sizes over periods exceeding a decade. *Branta* species typically graze on above-ground plant parts, a factor that might be expected to bring the population more gradually into balance with habitat carrying capacity. This contrast in *Branta* and *Anser* foraging behaviour might influence our interpretation of population dynamics in the two goose types.

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