Barnacle geese *Branta leucopsis* on Nordenskiöldkysten, western Spitsbergen—in thirty years from colonisation to saturation

RUDOLF H. DRENT, JEFFREY M. BLACK, MAARTEN J. J. E. LOONEN and JOUKE PROP

Drent, R. H., Black, J. M., Loonen, M. J. J. E. & Prop, J. 1998: Barnacle geese *Branta leucopsis* on Nordenskiöldkysten, western Spitsbergen—in thirty years from colonisation to saturation. Pp. 105–114 in Mehlum, F., Black, J. M. & Madsen, J. (eds.): Research on Arctic Geese, Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skrifter 200.*

Goose surveys on Nordenskiöldkysten, a 40-km stretch centred at 78°N on the western shoreline of Spitsbergen, were undertaken during 13 seasons in the period 1975–97. The surveys show that peak numbers of adults and goslings during the moult period July–August have flattened out since 1986. In agreement with predictions on grazing capacity of shoreline vegetation, the density of geese in the various lake systems has now converged to the same value throughout. This suggests that the lakeside tundra limits capacity during the flightless period when the geese are vulnerable to fox predation. The area was colonised for nesting in 1963, but despite the current stability in summer numbers, the nest counts on the three major breeding islets continue to rise. Gosling production from the study area has dropped in absolute terms since at least 1980, and this decline is viewed as evidence for density-dependence on the breeding grounds. Losses on the breeding islands and among very young goslings have risen dramatically and a plea is made for further research to identify the causal mechanisms behind these changes.

R. H. Drent, M. J. J. E. Loonen and J. Prop, Zoological Laboratory, University of Groningen, NL-9750 AA Haren, The Netherlands; J. M. Black, Wildfowl & Wetlands Trust, Slimbridge, Gloucester GL2 7BT, England, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K., (current address) Department of Wildlife, Humboldt State University, Arcata, California, 95521-8299, U.S.A.

Introduction

The idea that increases in animal populations are accompanied by check-and-balance mechanisms such as increased mortality, reduced production, emigration, or a combination of these, is now firmly entrenched as one of the key concepts in ecological theory (Sinclair 1989). The application of this concept of density dependence has practical implications for the management of goose populations now recovering from excessive mortality in the past as a result of hunting pressure and loss of foraging habitat. This is more fully discussed elsewhere (Ebbinge 1991; Black 1998, this volume; Loonen et al. 1998, this volume). Whether or not the population increase calls for active intervention by man is an issue that has attained prominence, not on account of the increasing conflicts with agricultural interests in the wintering and staging grounds, but more especially due to the large scale destruction of feeding habitat on the northern tundras by the geese themselves. This is a negative impact of the recovery of goose populations which the conservation movement worked so hard to achieve. The impact has been extensively documented for the lesser snow goose *Anser caerulescens caerulescens* at various localities in Arctic Canada (see review by Batt 1997) and has led to renewed interest on the stability of the interaction between geese and their food plants on the breeding grounds elsewhere. As a contribution to this debate, we here present census data covering the establishment and stabilisation of a barnacle goose *Branta leucopsis* summer population in a small but discrete coastal area in western Spitsbergen. Fates of marked individuals identified on catching expeditions in the study area in years 1977, 1981, 1986, 1989 and 1995 help narrow the search for factors responsible for demographic change.

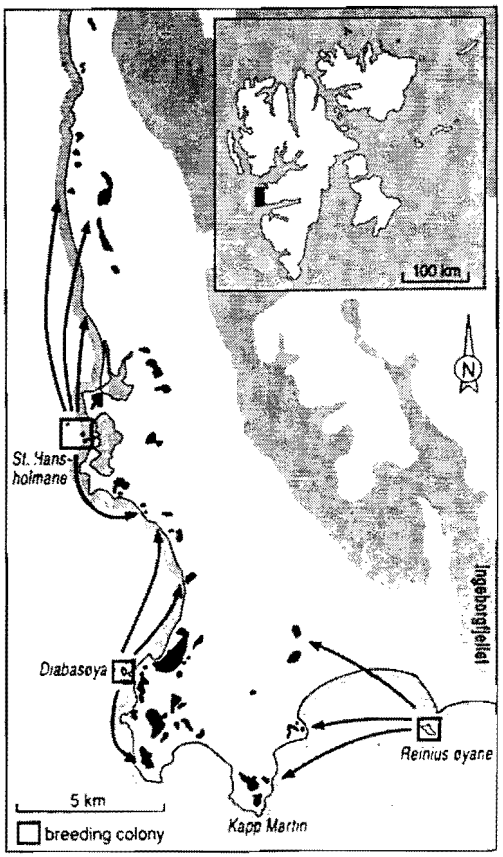

Fig. 1. Map of the Nordenskiöldkysten coastal plain study area bounded on the west by the ocean and to the east by steep mountains. Dispersal pattern of marked parents originating from the three nesting colonies (from Prop et al. 1980) define the counting sectors. Note the diffuse pattern of freshwater ponds and lakes on this tundra area.

Study area

The coastal plain extending 40 km from Isfjorden in the north to Bellsund in the south on the western shoreline of Spitsbergen is generally known as Nordenskiöldkysten (Fig. 1). Due to relative ease of access, this area is one of the best explored parts of the archipelago. To the north, the Isfjord radio station at Kapp Linné is manned year-round by a small crew, the only locality nowadays permanently inhabited along this coast. In the past, fur trapping was an important activity here, but with the closure of the polar bear hunt between 1970 and 1973 this activity has virtually ceased and the string of huts has since fallen into disrepair. In the early years of the century, mainly between 1908 and 1926, there was a flurry of geological exploration and tentative mining at the foot of Ingeborgfjellet and on one of the Reiniusøyane at the southern end of the area, and several cabins have survived (Hjelle 1993). Over the past twenty years, there has been very little human activity in summer aside from small field parties engaged in geological or biological survey and research and only occasional visits from small vessels (up to 1977 sealers).

The coastal plain is shaped like a triangle, 2 km wide towards Isfjorden and widening to 12 km at Bellsund (see Fig. 2). With the exception of a few low knolls generally less than 20 m, the elevation is broken only by old beach ridges which form gentle arcs in the landscape and are intersected by two major river systems, the Orustelva and Ytterdalselva which drain the inner valleys. Snow cover on the tundra falls to 50% by mid-June in early years and is delayed until early July in late seasons. The temperature in summer is rather stable and usually between 0 and 10°C (July mean at Isfjorden 4.7°C). Most precipitation in summer is in the form of drizzle but snow can fall in any month. Heavy overcast is the most prevalent weather condition, and especially in areas away from the direct influence of the fjord entrances, winds in summer are generally light; sea ice often packs along the coastline and in some summers persists well into August, impeding small boat traffic.

Foraging geese are mainly found in two habitats: the moss meadows encircling the lakes, and the fjellmark vegetation covering the higher elevations (see Prop & de Vries 1993). Moss meadows are usually restricted to narrow zones less than 5 m wide around the water bodies, though vaster meadows occur locally (for example around Holmungen, Oddvatna, Flosjøen and Eungane). Main food plants for the geese in the moss carpets are graminoids (*Dupontia* spp., *Poa* spp., *Festuca* spp., and *Carex subspathacea* on brackish sites). The fjellmark consists of a wide variety of soils and geological formations and is characterised by a low cover of plants. The fjellmark appears bare when viewed at a distance, but the old beach ridges in particular are colonised by lichens, providing sites vital for the geese where they feed on herbs (*Saxifraga* spp., *Draba* spp., *Cerastium* spp.) as well as on the buds of *Salix polaris* and the above-ground portions of horsetails *Equisetum* spp.

Two of the colony islands (Diabasøya and Reiniusøyane) were formerly linked to the mainland by a narrow ridge or spit, but around the 1940s this connection has been worn away by sea and ice action. However, these islands are still

Fig. 2. Aerial view of the Nordenskiöldkysten looking north with Isfjorden in the background. The colony site Diabas is in the foreground. The many lakes along the coastline can be seen as well as the old beach ridges further back, an important foraging habitat for the geese (Photo: Norsk Polarinstitutt, no. S36/1934).

covered by original tundra vegetation which provides foraging opportunities for some of the nesting geese. The other colony islands further north along the coast consist largely of barren rock with hardly any vegetation. Nesting common eiders *Somateria mollissima* as well as several nesting pairs of glaucous gulls *Larus hyperboreus* are found on all of the islands.

History of the barnacle goose on Nordenskiöldkysten

Løvenskiold (1964) reviews the early records and relates that before 1964 there was no proof of nesting on Nordenskiöldkysten. The oldest nesting colony established on this coast was first reported in 1964 when several barnacle goose families were observed close to St. Hansholmane. Breeding at Diabas was confirmed in 1968 when three nests were reported. Prestrud et al. (1989) presume that nesting at Reiniusøyane commenced at about the same time as well (1965), but the first documented count is from 1975 (Ebbinge & Ebbinge-Dallmeijer 1976). An early foot survey in June/July of 1964 attests to the fact that no barnacle geese had yet colonised on Nordenskiöldkysten (Norderhaug et al. 1965). More recently, a few pairs have nested on rocks off Båtodden (from 1975 on) and since 1996 several pairs have nested near the buildings of the Isfjord radio station and hatched their eggs successfully, surrounded by the many eider ducks that have nested in the vicinity since at least the 1950s. Norderhaug (1970) observed that island nesting was a relatively late development in the archipelago. In the 1950s and 1960s more birds were found on the offshore islands than on the traditionally used hillside sites further into the fjords.

Survey methods

The goose survey was conducted during the moult when adults and goslings are flightless. During this time the geese concentrate around the tundra pools where the grassy margins provide favoured feeding. The geese can retreat to the lakes themselves when danger threatens, such as approach by fox or humans. The preferred survey method was to traverse the coast on foot, walking the beaches and creeping up to view the lakes under the cover of driftwood, rocky outcrops or old beach ridges. Our intention was to register the number of adults and goslings associated with each lake, without disturbing the feeding flocks and this avoiding shifts to other sites, or causing the flocks to rush into the sea. The large interior lakes Stabbvatna and Holmungen required some ingenuity in completing the counts without causing wholesale shifts of the geese, and the judicious use of a 45×

telescope was essential. In most years the lakes were counted twice. The area near Kapp Martin was counted more frequently as the lakes Hustjørna and Fjørungen could be counted from the hut known as Gåsebu, which was erected in 1978 and also served as the cache for our expedition supplies. Typically, the counts were made by one by two observers working together, and the timing of the counts was subject to weather conditions as persistent fog could be a problem at that time of year. Counts during the moult are available from 1975, 1977–1979, 1980, 1981, 1986, 1989–1991, 1993, 1995, and 1997 (see Acknowledgements).

Working from portable hides in the intensive study period 1977–1981, observers camped in the area for four months each season, May through August. An effort was devoted to tracing the movements of parents with their goslings as they dispersed over the tundra lakes from the nesting colonies. The parents were individually marked with coded leg rings and recognisable at distances up to 300 m. The pattern of dispersal detected at that time (Prop et al. 1980, 1984) was assumed to hold throughout the survey period and will be used to assign goslings and parents to their respective colonies (Fig. 1).

After nesting colonies in the area were discovered in the late 1960s, the Ebbinges carried out a survey by boat along the coast. They counted all nests in 1975 (Ebbinge & Ebbinge-Dallmeijer 1976) in combination with Dittami, and helpers also engaged in goose work that season (Dittami et al. 1977, 1979). The rocky offshore islets identified as nesting areas in 1975 are still in use, and nest-count surveys by boat covered all sites in 1977, 1979–1981, 1986 and 1995, thus spanning a twenty-year period. Nest counts were performed post-hatch by traversing the island in a line abreast (generally not more than 5 m between observers) when nests could be distinguished from eider nests by examining egg shells and down.

After the bulk of the geese had departed, intensive work was carried out at the Diabas colony to provide a check on the effectiveness of a single nest estimate of the breeding population. From continuous observations from a tower on the mainland tundra opposite the island, the number of nests initiated was known exactly and could be compared to the total nests counted during inventory visits to the island later in the season. Although a substantial proportion of nests abandoned at an early stage were in fact missed during the island inventories, the overall recording covered on average 90% of all nests known to have been initiated. The effectiveness of the island survey varied somewhat from year to year depending on the numbers of pairs that had abandoned their nests early and on weather conditions that season. Counts on the island in relation to the total nest count from the continuous tower watches resulted in recovery of 91% (1979), 92.5% (1980) and 85% (1981 the year with a high rate of abandonment) of the total nests initiated that season. It can be concluded that a single nest inventory undertaken by experienced observers late in the season is unlikely to underestimate the number of nests initiated that season by more than 10%.

An important data source on composition and local distribution of the barnacle goose population resulted from catching expeditions to the Nordenskiöldkysten when moulting concentrations were rounded up for ringing. These expeditions involved seven or more observers and took place in 1977 (Owen et al. 1978), 1981, 1986, 1989 and 1995. Some catches were also executed on the wintering grounds in Scotland, where in most seasons an intensive programme on ring-reading on the marked individuals was carried through.

Results

The number of adult barnacle geese moulting on Nordenskiöldkysten has grown steadily over the past twenty years, but there is a suggestion that a plateau value is being approached as a quadratic fit is statistically a better fit than the linear fit (see the semi-logarithmic plot of Fig. 3 where a linear fit

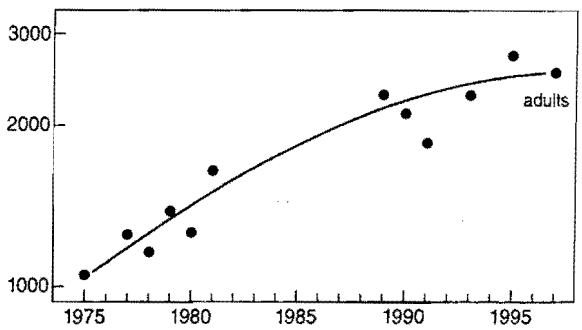

Fig. 3. Increase in numbers of barnacle geese counted along Nordenskiöldkysten during the moult, semi-logarithmic plot (ceiling value calculated by logistic growth approximation).

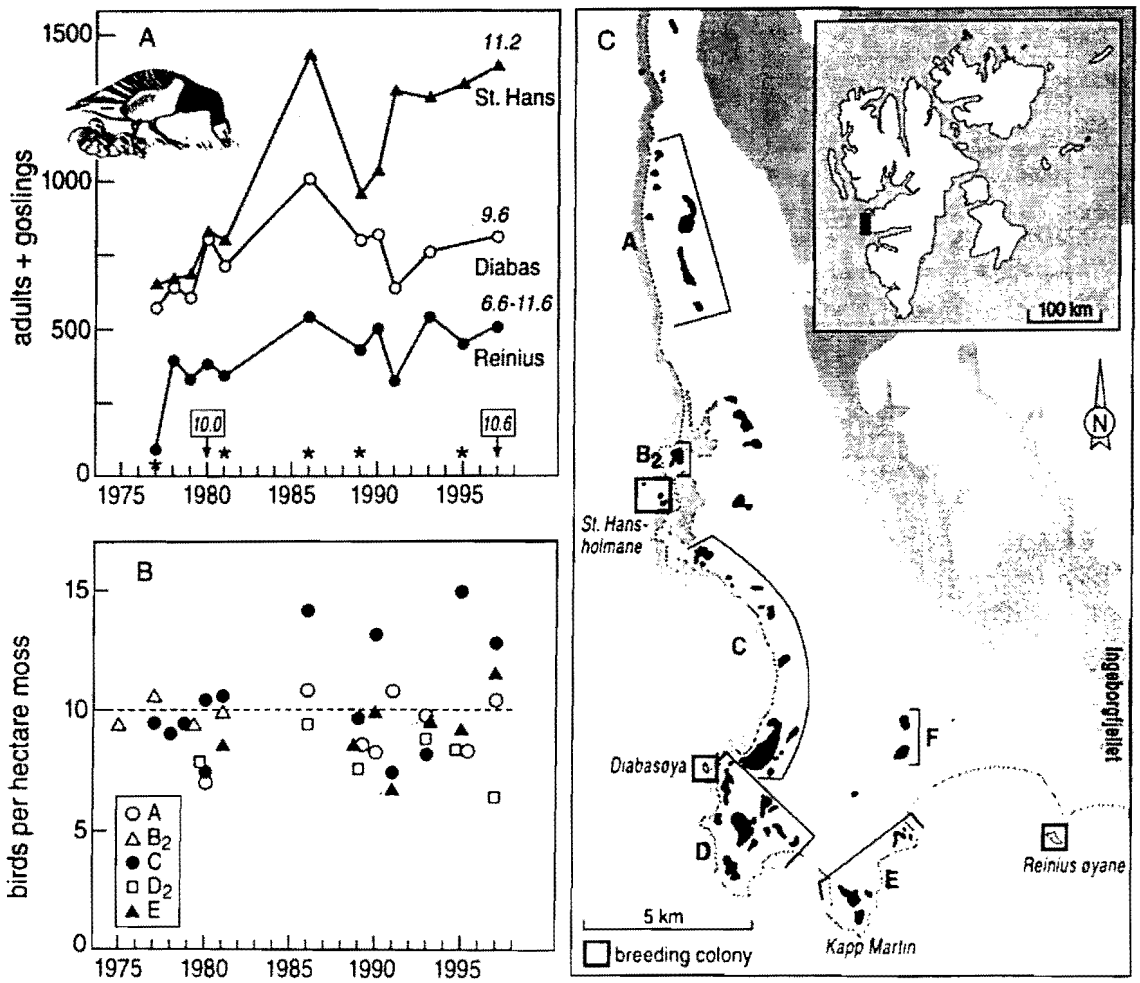

Fig. 4. Totals of adult and gosling barnacle geese (A) counted during moult per sector assigned to each colony according to Fig. 1. Note the plateau since 1986. (B) shows densities (geese per hectare suitable moss vegetation as ascertained by Prop et al. 1984) for selected tundra lake configurations (C) where broods congregate during moult indicate constant use throughout the period. See text for recruitment to new areas. Stars in panel A indicate catching expeditions.

would imply a constant rate of increase). Since we know the point of origin of the local population (here taken as 1964 = 0), a logistic growth curve fitted to the data would predict an asymptote at 2600–2800 adults. If this eventual ceiling limit is related to feeding conditions, it would perhaps be useful to consider all geese (adults and half-grown goslings, for example those surviving at least through early August, together). These data are shown in Fig. 4 and again the total goose count is very suggestive of a plateau value. We will return to this point in the discussion, as Prop et al. (1984) had previously recorded a prediction for the eventual capacity of the study area, extrapolating from the subunits thought by the early 1980s to be saturated. When the totals, adults and goslings together, are shown separately for the three colony tundra sectors (Fig. 4), it will be seen that nowhere have the counts of 1986 been exceeded in the six census years thereafter.

The number of goslings produced within Nordenskiöldkysten shows a steady absolute decline from 1980 onwards (Fig. 5A). In contrast, the number of nests in the colonies as determined from nest counts on the islands after hatch has increased during the same period (Fig. 5B). As shown by the breakdown in Fig. 5A, this decline has been noted in the tundra sectors associated with each of the three colony locations. The Reinius colony has contributed about 30% of all goslings counted on the moulting grounds throughout the period. It is not possible to trace events further back than 1975, the first complete tundra count (Ebbinge & Ebbinge-Dallmeijer 1977). In 1977 an intensive survey coincided with a failed season; less than 20 goslings were

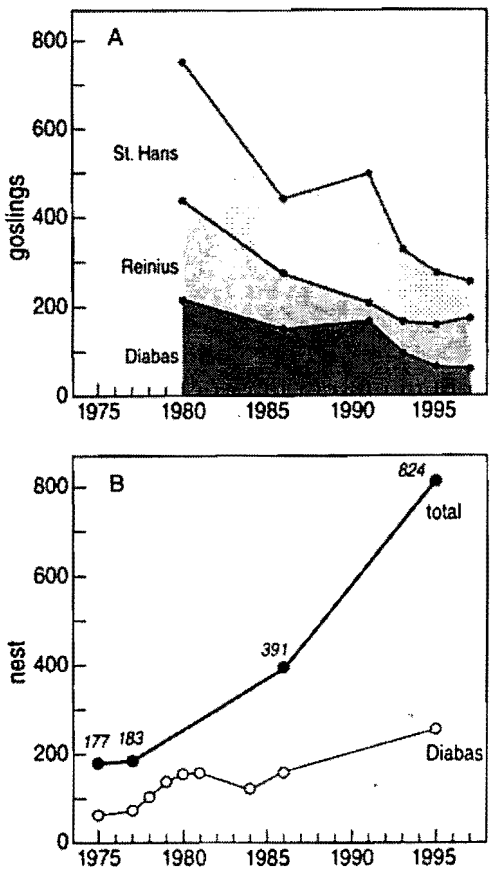

Fig. 5. Gosling production (A) and nest counts (B) for Nordenskiöldkysten barnacle geese. It will be noted that the Diabas colony was counted in more years than the others.

produced from a minimum of 177 nests (see Owen et al. 1978). The years 1979 and 1981 were also seasons of late snowmelt and low production (Prop et al. 1984) and are therefore not representative for reproductive potential at that demographic stage.

Fig. 6 shows the declining productivity in another way. From the catches in 1977 and 1981, at the start of the period, 1986 and 1989 roughly midway and in 1995 towards the end, the composition of the adult population is known. As can be seen, the proportion of yearlings in the catch declined sharply from approximately one-third in 1977 and 1981 (computed on the basis of full-grown geese caught) to a mere 2% in 1995 (see Fig. 6). From these data the number of goslings per adult female on Nordenskiöldkysten can be computed by taking the catch data as representative for the age distribution along the coast, subtracting the presumed number of yearlings from the total count of 'adults', and then dividing by two to obtain the female contingent two years or older; sex ratio in the adult catch was in fact close to equality. These computations indicate that 75% of the paired adults were associated with young in the tundra stage in 1980, but only 16% by 1995. Average production (young per nesting attempt surviving to well-grown tundra stage) also dropped steeply (see Fig. 6). The sharp decline in productivity since 1980 is also evident in the winter data from Caerlaverock, where brood size was determined for marked females of 2+ years old in large samples (also included in the figure). Paradoxically, an ever increasing adult goose population is producing fewer and fewer goslings.

Gosling survival to the wintering grounds in

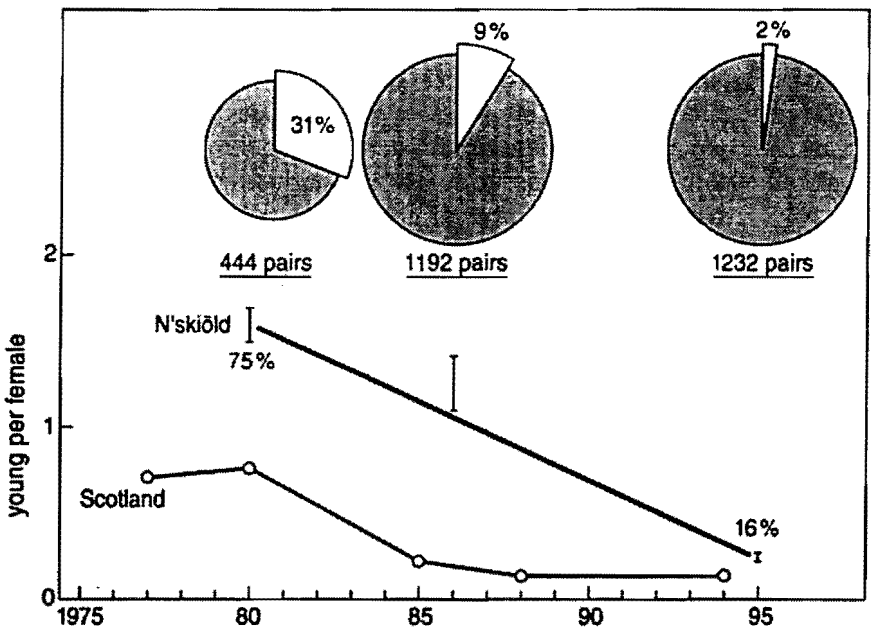

Fig. 6. Decline in productivity (goslings per female 2 years or older) of Nordenskiöldkysten barnacle geese determined during moult, compared with the same statistic upon arrival in Scotland (below) for the Svalbard population as a whole (from Black, Pettifor & Owen unpubl.). The pie diagrams present composition of the fullgrown population at Nordenskiöld kysten as determined from catches of flightless geese and show declining yearling segment (n = sample size).

Table 1. Survival of barnacle goose *Branta leucopsis* goslings from the breeding areas in Svalbard to the wintering grounds in Britain.

Survey years	Surviving goslings	Percentage survival	Source
1977	37/46	= 80.4%	(Owen & Black 1989, revised)
1978/1981	300/378	= 79.4%	(Prop et al. 1984)
1984*	172/195	= 88.2%	(Owen & Black 1989, revised)
1986	198/328	= 60.4%	(Owen & Black 1989, revised)
1989	35/60	= 58.3%	WWT files
1995	66/82	= 80.5%	WWT files

* not ringed on Nordenskiöld kysten.

Caerlaverock, Scotland, from age 4–6 months can be computed for the catch years where the figures give the percentage of juveniles individually marked on the breeding grounds and subsequently identified on the wintering grounds (Caerlaverock) (Table 1). Similarly in the seasons of intensive observation (1978 through 1981), family sizes of marked parents were ascertained close to departure from Spitsbergen (adults and goslings surviving through early August) as well as later at Caerlaverock.

Discussion

Events at Nordenskiöldkysten reflect on a small scale the demographic transition that has overtaken the Svalbard population of the barnacle goose. The decline in gosling production deserves the appellation catastrophic, as the sharp fall in goslings per adult female is almost 90% over the study period. Owen (1984) presented data on the number of juvenile barnacle geese reaching the

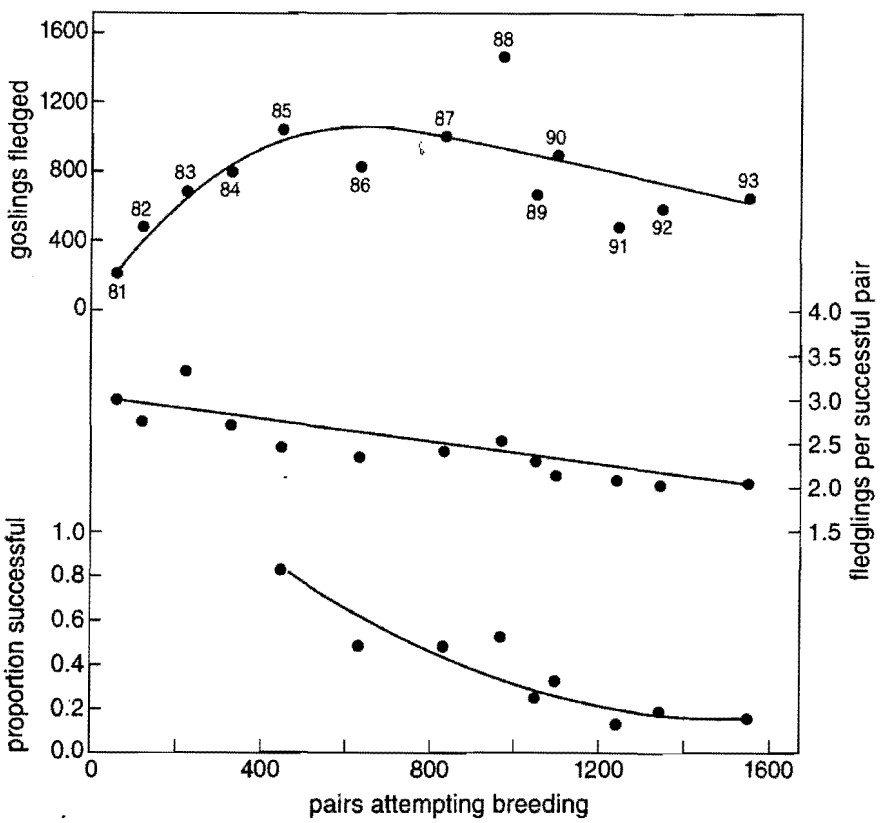

Fig. 7. Density effects in breeding output of the barnacle goose at the Laus Holmar site (Gotland, Sweden, colonised 1971) studied since 1981 by Larsson & Forslund (1994). The production of fledging geese (absolute numbers) peaks at intermediate colony size (upper curve) reflecting a steady decline in output of fledglings per successful pair (middle curve) and the overriding effect of the sharp fall in proportion of pairs laying eggs that fledge at least one gosling (lower curve). Assembled from Larsson & Forslund (1994).

Table 2. Shoot density of food plants on vegetation transects near Kapp Martin sampled over an interval of approximately ten years. Data refer to mean density of shoots in plots of 400 cm^2 (sample size indicated) as determined in earlier year (First, 1978 or 1980 as shown) and later (either 1988 or 1989).

Plant species	Locality*, years	Mean density		Sample size (n)	F statistic
		first yrs	later yrs		
Dupontia fisheri	V, 1980 and 1989	45.5	40.9	25	F (1,48) = 0.97
Dupontia fisheri	F, 1978 and 1988	52.4	49.2	32	F (1,62) = 0.06
Festuca spp.	F, 1978 and 1988	106.9	109.8	23	F (1,44) = 0.03
Carex subspathacea	V, 1980 and 1989	203.2	216.9	28	F (1,54) = 1.10

* V = Vinkelvatnet, F = Fjörungen.

supported by the observation of large numbers of geese in the area as soon as they have regained flight capability. A small lake west of the mouth of Ytterdalselva has been in use since 1993 and may hold up to 115 birds (vegetated area not measured). To the north of our sector A, geese have also started to nest in small numbers: During the moult in 1997, 16 adult geese and 16 goslings were observed at the margins of Linnévatnet, which commutes with the bay at Russekeila. Along the margins of the study area, there may thus be potential for slight enlargement of the summer capacity, but the prediction for the sectors A through F based on the counts for 1977–1981 was a total moult population of 2800 geese (excluding Eungane), and this value has been attained in both recent census years (2869 in 1995, 2600 in 1997).

How the local plant production in interaction with predation pressure sets this limit can only be determined by detailed future study, but we can at this stage already exclude the possibility of competition with other goose species. The pink-footed goose *Anser brachyrhynchus* breeds and summers in much smaller numbers on Nordenskiöldkysten and the most recent count (1997) executed under favourable conditions did not reveal more than 180 individuals utilising the same feeding areas alongside the barnacle geese. A quantitatively important competitive exclusion, as hinted for East Greenland by Madsen & Mortensen (1987), where the same two species are involved seems therefore unlikely in our case.

The constancy of goose grazing pressures argues against deleterious impacts of goose grazing on the vegetation when viewed over a twenty-year period on individual lake margins. This is particularly true in the brood-raising phase when the geese flocks are highly concentrated. Vegetation data, collected at an interval of a decade from transects at sites intensively grazed by barnacle geese, showed no change in density of the main food plants (Table 2). In both *Dupontia* transects, however, the moss carpet had been damaged locally (10% of the plots) by geese extracting tufts of moss in search of basal stems of their food plants. Clearly, monitoring of the vegetation will have to continue, and we hope to sample other transects from the early years in order to extend the sample.

Acknowledgements. – Observers contributing to the surveys in 1977, 1978, 1979, 1980 and 1981 are listed in Owen et al. (1978) and Prop et al. (1984); counts in 1986 were co-ordinated by J. M. Black, and undertaken by R. Drent in 1989, 1991, 1993, 1995 and 1997 (with the help of M. J. J. E. Loonen and V. Kalyakin in 1989 and of H. Drent in 1993, 1995 and 1997). Data from 1990 were supplied by I. Pokrovskaya. The unstinting logistic assistance by the Norsk Polarinstitutt and the Sysselmannen på Svalbard throughout has been a major incentive to continue the project, and we wish to mention specifically the help of F. Mehlum, P. Prestrud and the late K. Bratlien. The hospitality of the station personnel at Isfjord Radio has assumed legendary proportions as we look fondly back on all the help we have enjoyed since 1975. We acknowledge financial assistance from Groningen University and the Pieter Langenhuys Fonds.

References

Batt, B. D. J. (ed.) 1997: Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Arctic Joint Venture Special Publication, U.S. Fish & Wildlife Service, Washington, D.C. and Canadian Wildlife Service, Ottawa, Ontario, pp. 1–120.

Black, J. M. 1998: Movement of barnacle geese between colonies in Svalbard and the colonisation process. Pp. 115–127 in Mehlum, F., Black, J. M. & Madsen, J. (eds.):

Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skrifter 200*, this volume.

Black, J. M., Cooch, E. G., Loonen, M. J. J. E., Drent, R. H. & Owen, M. 1998: Body size variation in barnacle goose colonies: Evidence for local saturation of habitats. Pp. 129–140 in Mehlum, F., Black, J. M. & Madsen, J. (eds.): Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skrifter 200*, this volume.

Cooch, E. G., Lank, D. B., Rockwell, R. F. & Cooke, F. 1989: Long-term decline in fecundity in a Snow Goose population; evidence for density dependence? *J. Anim. Ecol. 58*, 711–726.

Cooch, E. G., Lank, D. B., Rockwell, R. F. & Cooke, F. 1991: Long-term decline in body size in a Snow Goose population: evidence of environmental degradation? *J. Anim. Ecol. 60*, 483–496.

Cooke, F., Rockwell, R. F. & Lank, D. B. 1995: *The Snow Geese of La Pérouse Bay: Natural selection in the wild.* Oxford Univ. Press.

Dittami, J., Thomforde, T. & Kennedy, S. 1977: Preliminary observations on the nesting of Barnacle Geese in Spitsbergen. *Wildfowl 28*, 94–100.

Dittami, J., Kennedy, S., & Thomforde, T. 1979: Observations on Barnacle Goose breeding, *Branta leucopsis*, in Spitsbergen 1975. *J. Orn. 120*, 188–195.

Ebbinge, B. S. 1991: The impact of hunting on mortality rates and spatial distribution of geese, wintering in the western palearctic. *Ardea 79*, 197–209.

Ebbinge, B. & Ebbinge-Dallmeijer, D. 1977: Barnacle Geese (*Branta leucopsis*) in the Arctic summer. *Norsk Polarinst. Årbok* 1975, 119–138.

Gadallah, F. L. & Jefferies, R. L. 1995: Forage quality in brood rearing areas of the Lesser Snow Goose and growth of captive goslings. *J. Appl. Ecol. 32*, 276–287.

Hjelle, A. 1993: Geology of Svalbard. Polarhåndbok No. 7, Norsk Polarinstitutt, Oslo, pp. 1–163.

Larsson, K. & Forslund, P. 1994: Population dynamics of the Barnacle Goose *Branta leucopsis* in the Baltic area: density-dependent effects on reproduction. *J. Anim. Ecol. 63*, 954–962.

Lessells, C. M. 1987: Parental investment, brood size and time budgets: behaviour in Lesser Snow Goose families. *Ardea 75*, 189–203.

Loonen, M. J. J. E., Tombre, I. M. & Mehlum, F. 1998: Development of an arctic barnacle goose colony: Interactions between density and predation. Pp. 67–79 in Mehlum, F., Black, J. M. & Madsen, J. (eds.): Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skrifter 200*, this volume.

Løvenskiold, H. L. 1964: Avifauna Svalbardensis. *Norsk Polarinst. Skr. 129*, 1–460.

Madsen, J. & Mortensen, C. E. 1987: Habitat exploitation and interspecific competition of moulting geese in East Greenland. *Ibis 129*, 302–303.

Mulder, R. S., Williams, T. D. & Cooke, F. 1995: Dominance, brood size and foraging behavior during brood-rearing in the Lesser Snow Goose: an experimental study. *Condor 97*, 99–106.

Newton, I. 1998: *Population limitation in Birds*, Academic Press, London, pp. 1–597.

Newton, I. & Kerbes, R. H. 1974: Breeding of Greylag Geese (*Anser anser*) on the Outer Hebrides, Scotland. *J. Anim Ecol. 43*, 771–783.

Norderhaug, M. 1970: The present status of the Barnacle Goose (*Branta leucopsis*) in Svalbard. *Norsk Polarinst. Årbok 1968*, 24–35.

Norderhaug, M., Ogilvie, M. A. & Taylor, R. J. F. 1965: Breeding success of geese in west Spitsbergen, 1964. *Ann. Rep. Wildfowl Trust 16*, 106–110.

Owen, M. 1984: Dynamics and age structure of an increasing goose population—the Svalbard Barnacle goose *Branta leucopsis. Norsk Polarinst. Skr. 181*, 37–47.

Owen, M. & Black, J. M. 1989: Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. *J. Anim. Ecol. 58*, 603–618.

Owen, M., Drent, R. H., Ogilvie, M. A. & Van Spanje, T. M. 1978: Numbers, distribution and catching of Barnacle Geese (*Branta leucopsis*) on the Nordenskiöldkysten, Svalbard, in 1977. *Norsk Polarinst. Årbok 1977*, 247–258.

Owen, M. & Norderhaug, M. 1977: Population dynamics of Barnacle Geese *Branta leucopsis* breeding in Svalbard, 1948–1976. *Ornis Scand. 8*, 161–174.

Prestrud, P., Black, J. M. & Owen, M. 1989: The relationship between an increasing Barnacle Goose *Branta leucopsis* population and the number and size of colonies in Svalbard. *Wildfowl 40*, 32–38.

Prop, J. & de Vries, J. 1993: Impact of snow and food conditions on the reproductive conditions of the reproductive performance of Barnacle Geese *Branta leucopsis. Ornis Scand. 24*, 110–121.

Prop, J., van Eerden, M. R., Daan, S., Drent, R. H., Tinbergen, J. M. & St. Joseph, A. M. 1980: Ecology of the Barnacle Goose (*Branta leucopsis*) during the breeding season: Preliminary results from expeditions to Spitsbergen in 1977 and 1978. Pp. 51–112 in van Holk, A. G. F., St. Jacob, H. K. & Liefferink, E. H. (eds.): Spitsbergen Symposium. Proceedings of the Norwegian-Netherlands Symposium on Svalbard. Arctic Centre. University of Groningen.

Prop, J., van Eerden, M. R. & Drent, R. H. 1984: Reproductive success of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, Western Spitsbergen. *Norsk Polarinst. Skr. 181*, 87–117.

Sinclair, A. R. E. 1989: Population regulation of animals. Pp. 197–241 in Cherett, J. M. (ed.): *Ecological Concepts.* Blackwell, Oxford.

Williams, T. D., Cooch, E. G., Jefferies, R. L. & Cooke, F. 1993. Environmental degradation, food limitation and reproductive output: juvenile survival in Lesser Snow Geese. *J. Anim. Ecol. 62*, 766–777.