

Development of an arctic barnacle goose colony: Interactions between density and predation

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The development of a barnacle goose *Branta leucopsis* colony established in 1980 was studied from 1989 to 1997 using sightings of marked individuals. The number of adult geese was calculated using a Petersen estimate. Alternatively, the number of adult geese was based on estimates of gosling production and local return rate based on Jolly-Seber models. Both methods showed similar results and were close to censuses in 1996 and 1997. The local population increased rapidly up to 1993. Thereafter the growth rate levelled off, due to a decrease in both local return rate and gosling production. The local return rate was lower for goslings than for adults and females were more philopatric than males. The production of goslings was related to the presence of arctic foxes *Alopex lagopus* in the area. In the period 1992–95, predation by arctic foxes lowered the number of fledged goslings and moreover resulted in local crowding which had a negative effect on the growth rate of goslings and adult body condition. This density dependence was related to the presence of arctic foxes. Comparing years without foxes, before 1992 and after 1995, the population showed a three-fold increase but there was no difference in gosling production or gosling growth.

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Introduction

The regulation of animal numbers is the central theme in population studies: are populations limited by predation pressure, diseases, space, food availability or any combination of these factors? When the magnitude of these factors depends on population size, density dependence occurs and the population size will stabilise at equilibrium (Nicholson 1933; Lack 1966).

While most goose populations in Western Europe and North America have increased tremendously in the last decades (Ebbinge 1985; Madsen 1991), there has been a growing concern about future population size. Conflicts with farmers about goose damage on wintering and spring staging grounds are already widespread (Groot Bruinderink 1989; Owen 1990; Patterson 1991; Black 1998) and locally geese are able to destroy the vegetation on their arctic breeding

grounds (Kerbes et al. 1990; Kotanen & Jefferies 1997).

The explanation for the increase in population size are related to changes on the wintering and spring staging grounds. The use of artificial fertilizers has improved the fields used for winter and spring grazing and has provided the geese with a seemingly unlimited supply of good quality grasses. As a consequence, most goose species have shifted to agricultural land and expanded their winter feeding range (Madsen 1987; van Eerden et al. 1996). Together with a decrease in hunting pressure, as a result of hunting legislation, the establishment of nature reserves, and a reduction of the number of hunters (Ebbinge 1991), the winter and spring mortality of geese have decreased (Ebbinge 1991; Francis et al. 1992).

Reproductive success on the breeding grounds may eventually become more important for determining a maximum population size (Larsson & Forslund 1994) and is affected by food

availability and predation. Competition for food reduces the growth and survival of goslings (Cooch *et al.* 1991; Williams *et al.* 1993; Gadallah & Jefferies 1995) and predation pressure varies from year to year (Summers 1986).

Breeding on Svalbard and wintering in south-west Scotland, the Svalbard barnacle goose *Branta leucopsis* has a distribution distinct from the other three barnacle goose populations in the world. With a population size of less than 300 individuals in 1948, increasing to 23,000 individuals in 1996, this population is a prime example of the success of conservation measures (Black 1998). A hunting ban and the creation of a goose reserve at Caerlaverock, Scotland, has resulted in a great increase in the survival rate of wintering geese (Owen 1982). However, observations from the wintering grounds indicate that reproductive success per individual decreased as the population grew larger. The mean brood size on the wintering grounds, the fraction of the adult population accompanied by juveniles and the survival of adults in the period from March to September declined (Owen & Black 1991; Rowcliffe *et al.* 1995; Pettifor *et al.* 1998, this volume). At the end of the 1980s, the population size seemed to stabilise at 14,000 individuals. However, after 1992, the population increased rapidly to 23,000 individuals (1996) and the mechanism behind this rapid increase is being scrutinised (Black 1998; Pettifor *et al.* 1998).

Is there evidence for an increased competition for food on the breeding grounds of the Svalbard barnacle goose population? In Svalbard, both the density of nests in individual colonies and the number of known colonies has increased with the increase in population numbers (Prestrud *et al.* 1989; Mehlum 1998, this volume). Competition for food and predation might be different in each colony and this process needs to be studied on a colony scale.

This paper focuses on the population dynamics of a relatively newly established barnacle goose colony in Kongsfjorden. Local return rate of ringed individuals and the survival of goslings in recognisable families are extrapolated to the whole colony. It will be shown that arctic foxes *Alopex lagopus* played a major role in the population dynamics, both by killing goslings and restricting the feeding range of the geese. There is as yet no evidence for density dependence in this colony if the effect of the presence of predators is excluded.

Material and methods

Study area and population

No records exist of barnacle geese in Kongsfjorden from the early 1960s. In the years 1977 and 1978, a moulting flock of barnacle geese was sighted in Kongsfjorden (P. Prestrud, unpubl.) and the first record of a breeding barnacle goose is from 1980. Since 1980 the breeding population has increased rapidly, to 329 nests in 1997 (Tombre *et al.* 1998a, this volume). Barnacle geese breed on the islands in Kongsfjorden, and in years without arctic foxes some nests are also found in the vicinity of the village of Ny-Ålesund. After hatching of the eggs, most geese leave the breeding islands and move to the nearby mainland to feed, moult and raise their young. As the adults are flightless during wing moulting, the geese stay in the fjord until wing moulting is completed. The largest concentration of both goose families and adults without goslings is in the direct vicinity of Ny-Ålesund (Stahl & Loonen 1998, this volume).

In 1987, geese of the Kongsfjorden colony were caught for the first time during wing moulting. In 1989 there was a second catch, and in the period 1991–97 several catches were made each year. All geese caught were ringed with steel rings and individually coded plastic rings which can be read with a telescope to a distance of 200 metres.

Population size

A modified Petersen estimate was used to calculate the total number of adult geese in the population (Seber 1973). During the moulting period, the mortality of adult geese is almost zero (only two observations in seven years of study), and immigration and emigration during this phase are low because all geese are flightless. Therefore, the adult population was considered closed with a constant number of adult geese over the moulting period. Individuals which were recognisable by rings from previous years formed the marked population (r). We assumed that all ringed geese present in the Kongsfjord area were read and that there was an equal chance of catching families from the marked population as from the unmarked population. For each catch (i), the total number of

caught adults (n_i) and the number of caught adults which had been recognisable due to rings from previous years (m_i) were counted. The estimate for the number of adult geese in the population was then $N = r \cdot \sum n_i / \sum m_i$. A conservative confidence interval of the population estimate was calculated by using a normal approximation without taking the sampling fraction into account (Seber 1973). The sampling fraction ($\sum n_i / N$) was in some years larger than one because several individuals were captured twice in a season. In 1990, no catches were made and the ring percentage is based on sightings.

To estimate the total number of families, all recognisable families, with at least one parent ringed, formed the marked population. For the proportion of marked families, we used the number of marked individuals identified at the nest during incubation, divided by the total number of nests where rings of parents were checked.

In 1996 and 1997, the whole fjord was censused in the last week of June in order to obtain an assessment of the total adult population.

Gosling production

Barnacle goose goslings fledge when they are approximately 45 days old. The total number of fledged goslings in the population was estimated as the product of the mean number of fledged goslings per recognisable families and the total number of families in the population. A family was defined as two adult geese which have been sighted at least once with goslings. Family size was recorded at every sighting of a family which was recognisable by at least one ringed parent.

First, the number of fledged young from recognisable families was calculated. From all first sightings of recognisable families in a specific year, the number of goslings was summed and the average date of first sighting was calculated. A daily survival rate (DSR) was calculated from all sightings using a modified Mayfield technique allowing for brood mixing and dependence among brood mates (Flint et al. 1995). Variation in DSR across days was examined by estimating a separate DSR for each day. These values for DSR were regressed against date with the number of exposure days as a

weighting factor (Flint et al. 1995). A survival estimate from first observation till fledging (S_{fledge}) can be calculated by multiplying the daily values for DSR over the period from first observation until fledging. The date of fledging was calculated as 45 days after the annual average hatch date. The number of fledged goslings in recognisable families is the multiplication of the number of goslings at first sighting and the survival estimate S_{fledge} .

With an estimate for the total number of families in the population, the totals for all recognisable families could be extrapolated to the whole population.

Local return rate

Annual rates for local return rate and resighting were estimated from Jolly-Seber models of sightings of ringed individuals in Kongsfjorden. In 1989, a catch of 93 individuals was the first marking occasion. Goose rings were read intensively in all years from 1990 to 1997, while new individuals were ringed annually in the period 1991 to 1997. In the nine years of study, 701 individuals ringed as goslings and 732 individuals ringed as adults were used in the analysis. Mortality of first-year birds is higher than in adults (Owen & Black 1989), and philopatry to the natal colony differs between sexes, as is generally true for waterfowl (Anderson et al. 1992). Therefore, to allow testing for differences with sex and two age classes, the data were organised in four different sets and analysed simultaneously: males ringed as goslings, females ringed as goslings, males ringed as adults, and females ringed as adults. The first age class comprised individuals ringed as goslings with the possibility of returning as yearlings. The other age class consisted of older birds: those ringed as goslings from age 1 year onwards and all geese ringed as adults. In 1990 no catches were made, while in 1994 no goslings were caught due to an almost complete nest failure. Therefore, local return rate and resighting estimates for the first-year age class are not available for 1991 and 1995. Maximum-likelihood estimates were obtained using the program SURGE (Lebreton et al. 1992; Cooch et al. 1997). A complete hierarchy of time-dependent models from $\phi_{sat} p_{sat}$ to ϕ, p were estimated, where ϕ denotes local return

Table 1. Estimation of the number of adult barnacle geese in Kongsfjorden based on the density of geese ringed in previous years. The total number of previously ringed geese observed in the season is divided by the proportion of previously ringed geese in catches. ¹Extrapolation on account of restricted observation period in that year. ²Based on sightings.

Year	Caught with ring (<i>n</i>)	Total caught (<i>n</i>)	Ringed proportion (<i>p</i>)	Sighted rings from previous years (<i>r</i>)	Estimated population size ($N = r/p$)
1989	24	68	0.35	63 ¹	180
1990	221 ²	425 ²	0.52	102	196
1991	98	250	0.39	96	246
1992	166	304	0.55	264	480
1993	174	277	0.63	377	598
1994	108	171	0.63	390	619
1995	148	228	0.65	396	609
1996	201	333	0.60	432	720
1997	71	135	0.53	415	783

probabilities, *p* denotes resighting probabilities and *s*, *a* and *t* indicate respectively sex, age and time dependency. Logistic constraints were applied to the estimated parameters so that estimated local return rate and resighting probabilities were constrained in the range 0 to 1. Standard errors and confidence intervals around estimates were based on logit^{-1} transformations of the transformed values; confidence intervals are thus asymmetric. Model selection was done on the basis of Akaike's information criterion (AIC), calculated as the deviance of the model plus twice the number of parameters.

The population trend is calculated by multiplying the number of adults and goslings in year *t* with the local return rate of female adults and female goslings from year *t* to year *t* + 1. Because there is no indication for a trend in sex ratio of unringed adults over the years, we assume that a potential sex bias in philopatry is in equilibrium with immigration from other colonies of the opposite sex.

Gosling growth and grazing pressure

A growth curve for gosling weight was calculated using hierarchical linear modelling and age data of goslings as described in Loonen *et al.* (in press). Age, age² and year were the only independent variables entered in the model. Years

were grouped when there was no significant difference between years. Annual variation in growth rate is expressed by referring to the calculated average gosling weight at age 35 days.

The mossy shore of the lake Solvatnet (3.5 ha) within the village of Ny-Ålesund had the highest goose density of all sites. Grazing pressure was calculated from daily counts of adults, the average number of young per adult and the average body mass for adults and goslings. Average body mass for goslings was calculated from the annual growth curve. For each day, body mass of adults and goslings were multiplied with the number of adults and goslings to obtain an overall measure for grazing pressure (kg goose per ha). These data were averaged per 10-day period.

Results

Population size

The barnacle goose population in Kongsfjorden was estimated to 180 adults in 1989. From 1991 to 1992 the population almost doubled in size, but this rapid rate of increase was not maintained. The population hardly grew in the period 1993–95 but increased slowly after these years (Table 1). The observed number of adults from a census in the whole fjord was 679 adults in 1996 and 682 adults

Table 2. The number of families in the population during the flightless period as estimated with a Petersen estimate. The marked population are all observed families with at least one of the parents ringed at the start of the season. The proportion of recognisable pairs is based on data from nest checks.

Year	Recognisable and seen on nest (<i>n</i>)	Number of checked nests (<i>m</i>)	Proportion recognisable pairs (<i>p</i>)	Recognisable families seen (<i>r</i>)	Population estimate (<i>N</i>)
1990	29	43	0.67	41	61
1991	20	30	0.67	50	75
1992	80	126	0.63	77	122
1993	137	214	0.64	132	206
1994	10	13	0.77	13	17
1995	69	94	0.73	173	237
1996	106	129	0.82	188	229
1997	141	180	0.78	156	200

Table 3. Mean daily survival rates (DSR) of goslings in recognisable families in different years. Standard errors of DSR are smaller than 0.003. There is a significant positive trend in DSR over the rearing period in the years 1995, 1996 and 1997. In the regression equation day is expressed as July days (1 = 1 July).

Year	DSR	<i>F</i>	<i>P</i>	Regression
1990	0.9985	$F_{1,59} = 1.07$	0.305	
1991	0.9963	$F_{1,55} = 0.28$	0.596	
1992	0.9762	$F_{1,55} = 1.20$	0.279	
1993	0.9626	$F_{1,56} = 0.61$	0.438	
1994	0.9353	$F_{1,22} = 2.25$	0.148	
1995	0.9784	$F_{1,51} = 6.08$	0.017	$0.96868 + 0.00037 \cdot \text{day}$
1996	0.9944	$F_{1,51} = 7.07$	0.010	$0.98717 + 0.00024 \cdot \text{day}$
1997	0.9901	$F_{1,50} = 20.03$	0.000	$0.98166 + 0.00033 \cdot \text{day}$

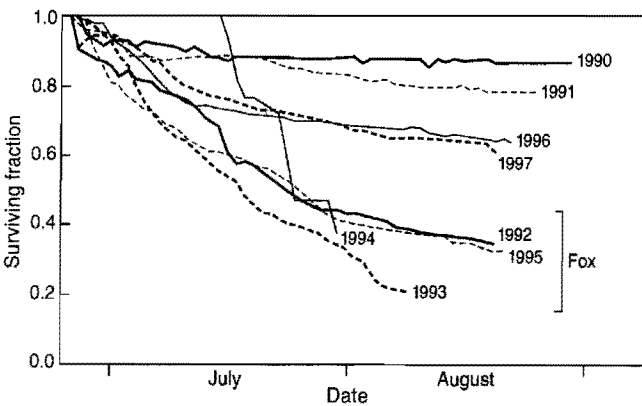


Fig. 1. The surviving fraction of goslings against date for different years. The surviving fraction is calculated by multiplying daily survival rates. There is a clear distinction between years with and without arctic foxes.

in 1997. The number of pairs with goslings showed a similar pattern and increased from 61 to 206 families in the period 1990–93, while there was very little increase in the period 1993–97

(Table 2). In 1994, very few families were observed because arctic foxes had access to the breeding islands during nest initiation and nearly all the nests were preyed on.

Table 4. Observed brood sizes of recognisable families at the first observation after hatching of the eggs, at the last observation, just before fledging and the proportion of families loosing all goslings before fledging. In the years 1990–91 and 1996–97 no foxes were present in the study area. In the period 1992–95 foxes were present. The year 1994 was almost a complete nest failure, because fast-ice enabled foxes to enter the main breeding islands. Hatching of eggs was very late in this year.

Year	Average family size at first observation		Average family size at last observation		Pairs loosing all goslings		Average date of observation
	avg	(st. dev)	avg	(st. dev)	n	%	
1990	3.27	(1.41)	3.13	(1.44)	40	1	24 Aug
1991	3.56	(1.38)	3.19	(1.40)	64	2	17 Aug
1992	3.25	(1.82)	2.00	(1.26)	57	27	16 Aug
1993	2.96	(1.14)	1.88	(1.23)	64	52	3 Aug
1994	1.91	(0.90)	1.67	(0.94)	6	5	27 July
1995	3.10	(1.37)	2.33	(1.32)	129	43	8 Aug
1996	3.28	(1.17)	2.96	(1.32)	160	14	17 Aug
1997	3.32	(1.05)	3.01	(1.19)	102	19	6 Aug

Gosling production

The daily survival rate of goslings differed between years (Table 3) and was clearly affected by the presence of the arctic fox. The local population of arctic foxes was not enumerated, but the difference between years was obvious. No foxes were observed in the period when the geese are flightless in the surroundings of Ny-Ålesund in 1990, 1991, 1996 and 1997, while we repeatedly saw patrolling foxes in the period 1992–95. In these years, gosling predation was observed on several occasions. The surviving fraction of goslings clearly reflected the difference in predation pressure between years with and without foxes (Fig. 1). While the arctic fox is the only identified predator after the goslings have reached the mainland, the glaucous gull *Larus hyperboreus* is an important predator on the breeding islands shortly after egg hatching. In the years 1995, 1996 and 1997, there was a linear increase in the daily survival rate over the season. In the other years no significant trend was found (Table 3).

The average number of goslings per family at the first sighting varies from a low of 1.9 in 1994 to a high of 3.6 in 1991, while all other values range from 3.0 to 3.3 goslings per pair. The fraction of families which have lost all goslings and the average family size of the geese at the last

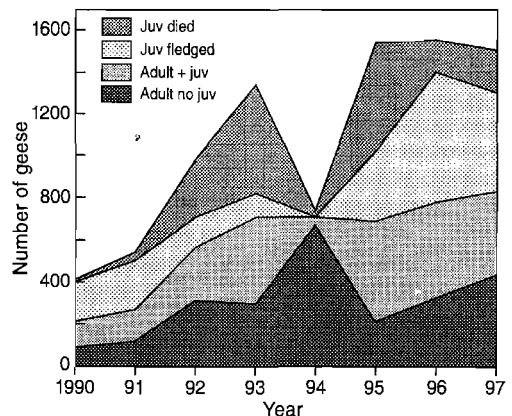


Fig. 2. The development of the barnacle goose population in Kongsfjorden, based on Petersen estimates. The adult birds are divided in those with and without hatching goslings. The number of goslings is divided in those dying before fledging and those surviving until fledging.

Table 5. The total number of goslings at hatching, catching and fledging for the Kongsfjorden population of barnacle geese in different years. The values are calculated from the average family size at first observation of recognisable families. The surviving fraction S is calculated using values for daily survival rate DSR as given in Table 5. Date is expressed as July days (1 = 1 July). ¹No value available, average value over all years used.

Year	Families with sightings	Estimated total number of families	Goslings seen at first obs.	Estimated total number goslings at first obs.	Average date hatching	Average date first obs.	Average date catching
1990	41	61	134	199	7.3	10.4	36.1 ¹
1991	66	75	235	267	6.2	11.9	33.0
1992	84	122	273	397	8.0	10.1	39.1
1993	116	206	343	609	6.9	7.8	35.3
1994	11	17	21	33	18.6	19.9	
1995	172	237	533	734	6.5	12.0	36.4
1996	174	229	571	752	9.6	13.4	34.4
1997	121	200	388	641	8.0	10.5	38.6

Year	$S_{hatch-first}$	Number of goslings at hatching	$S_{first-catch}$	Number of goslings at catching	$S_{first-fledg}$	Number of goslings at fledging
1990	0.9955	200	0.9617	192	0.9389	187
1991	0.9780	273	0.9251	247	0.8654	231
1992	0.9530	416	0.4973	197	0.3550	141
1993	0.9626	633	0.3573	218	0.1869	114
1994	0.9353	35			0.0527	2
1995	0.8693	845	0.5826	428	0.4431	325
1996	0.9704	774	0.8616	648	0.8255	620
1997	0.9556	671	0.7562	485	0.7251	465

Table 6. Resighting rate (p) and local return rate (ϕ) of barnacle geese as a function of time (t), sex (s) and age (a) using capture-resighting data and program SURGE. NP = number of identifiable parameters, DEV = deviance, AIC = Akaike's Information Criterion. Model 7 has the lowest value for AIC and is selected as the final model, with effects of sex, age and time on local return rate and effects of age and time on local resighting rate.

Model		NP	DEV	AIC
1	ϕ, p	2	5621.07	5625.07
2	$\phi, p(t)$	9	5384.29	5402.29
3	$\phi(t), p$	9	5370.66	5388.67
4	$\phi(t), p(t)$	15	5353.64	5384.64
5	$\phi(at), p(t)$	21	4994.96	5036.96
6	$\phi(at), p(at)$	26	4963.35	5015.35
7	$\phi(sat), p(at)$	40	4889.04	4969.04
8	$\phi(sat), p(t)$	35	4920.28	4990.28
9	$\phi(sat), p(sat)$	52	4872.26	4976.26

observation again clearly reflect the presence of the arctic fox (Table 4). The total gosling production varies from 2 goslings in 1994 to 620 in 1996 (Table 5). Fig. 2 shows the population size of adults and goslings in the Kongsfjorden population over the period 1990–97. The year

1994 is exceptional with almost no goslings because almost all nests were subject to predation, but over the entire study period, both the size of the adult population and the total population size of adults and goslings after hatching of the eggs were levelling off.

Table 7. Estimates for local return rate and resighting for barnacle geese in Kongsfjorden. Between brackets, the 95% confidence interval is given. ^aNo goslings ringed in 1990, ^bno goslings produced in 1994.

Year	Local return rate				Resighting		
	Male 1 year	Male adult	Female 1 year	Female adult	1 year	1 year	Adult
1990	0.24 [0.08,0.54] _a	0.90 [0.74,0.96]	0.23 [0.08,0.52]	0.85 [0.68,0.94]	0.65 [0.25,0.91]	0.93 [0.82,0.97]	
1991		0.88 [0.76,0.95]	_a	0.99 [0.75,1.00]		0.92 [0.85,0.96]	
1992	0.38 [0.28,0.48]	0.93 [0.86,0.97]	0.88 [0.78,0.94]	0.91 [0.83,0.95]	0.78 [0.69,0.86]	0.86 [0.81,0.91]	
1993	0.38 [0.24,0.55]	0.88 [0.82,0.93]	0.50 [0.36,0.64]	0.96 [0.91,0.99]	0.59 [0.43,0.73]	0.85 [0.81,0.88]	
1994	0.27 [0.13,0.49] _b	0.81 [0.75,0.86]	0.40 [0.24,0.57]	0.83 [0.78,0.88]	0.81 [0.55,0.94]	0.88 [0.85,0.91]	
1995		0.83 [0.77,0.87]	_b	0.81 [0.76,0.86]		0.89 [0.85,0.92]	
1996	0.39 [0.26,0.55]	0.82 [0.75,0.87]	0.49 [0.36,0.63]	0.85 [0.79,0.89]	0.72 [0.55,0.85]	0.94 [0.90,0.97]	

Local return rate

Table 6 shows the various models which were compared in this study. In the final model local return rate varied with age, sex and time and resighting rate varied with age and time. Local return rate estimates over the period 1989 to 1996 for two age classes and two sexes are given in Fig. 3 and Table 7. For geese ringed as goslings, local return rate in the first year is higher for females than for males (Δ deviance = 50.54, $df = 5$, $P < 0.001$). The difference is largest in 1991, when 88% of the females returned and only 38% of the males. In later years, the difference is on average 12%. For adult geese, there was also a significant difference in local return rate (Δ deviance = 17.49, $df = 8$, $P = 0.025$): 86% of the males returned while 89% of the females returned. The estimates for local return rate in adults show a decline over the years. Although this trend is non-significant, it will affect the calculated population size.

In the final model for local return rate, the resighting rate of all geese was year-specific. The resighting rate differed between adults and birds ringed as gosling in their first year after ringing (Δ deviance = 31.241, $df = 5$, $P = 0.000$). There was no significant difference between sexes in resighting possibility (Δ deviance = 16.776, $df = 12$, $P = 0.158$). The resighting rate varied from 0.52 to 0.81 for yearlings (ringed as gosling), and from 0.85 to 0.94 for adults (Table 7). The population trend calculated with the Petersen

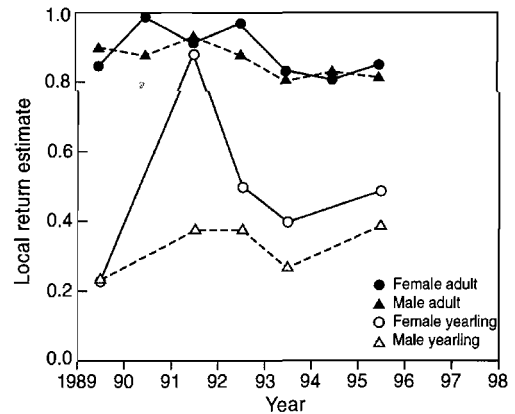


Fig. 3. Local return rate of barnacle geese to the Kongsfjorden area in different years, per sex and age.

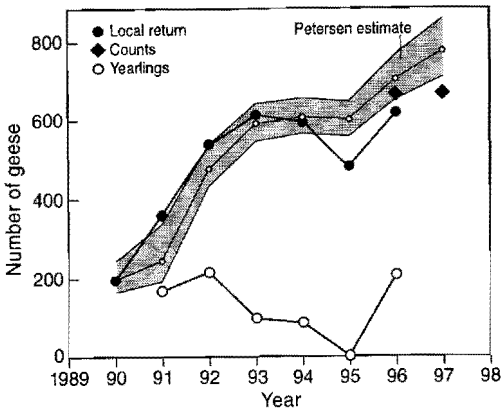


Fig. 4. The barnacle goose population in Kongsfjorden. Petersen estimates for each year are compared with a population trend based on local return rates and gosling production. In 1996 and 1997, the number of adults was also counted in the entire fjord (◆).

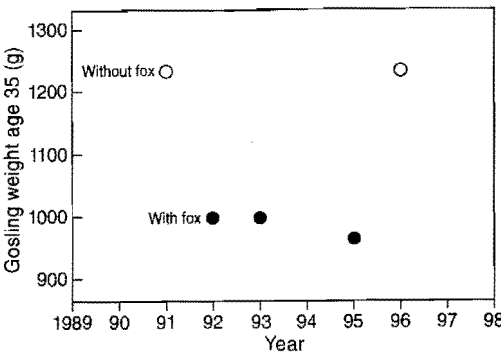


Fig. 5. Body mass of goslings at age 35 days in different years as calculated from growth curves. In years without arctic foxes, body mass is over 200 gram heavier than in years when arctic foxes are present.

estimate matches with the trend calculated from the local return rate and the total number of goslings produced (Fig. 4).

Grazing pressure and gosling growth

The weight of the goslings differed enormously between fox and non-fox years (Fig. 5). In a year without foxes, the goslings were on average 245 grams heavier than in years when foxes were present in the study area.

The grazing pressure on the shores of the lake

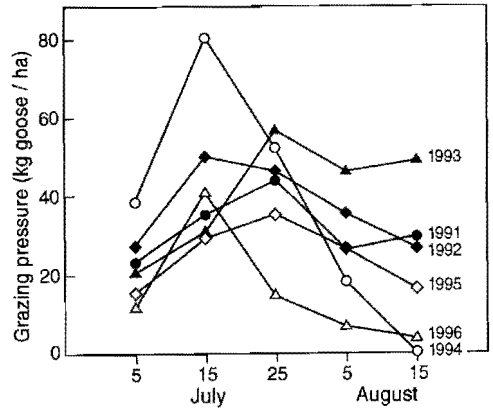


Fig. 6. Grazing pressure of barnacle geese on the shore of the lake, Solvatnet, the site with the highest goose density in Kongsfjorden. Grazing pressure is expressed as the combined body mass of adults and goslings present.

Solvatnet increased slightly in the period 1991–93 from 31 to 41 kg goose/ha. In 1993–96 there was a clear decreasing trend in grazing pressure, with an average grazing pressure in 1996 of only 16 kg goose/ha. In 1994, there were almost no families. Non-breeders and failed breeders moulted earlier (Loonen 1997) and most geese left the area after fledging in the end of July. In 1993, the grazing pressure was highest in August. This reflected the concentration of the geese close to safe water as a reaction to the constant presence of foxes (Stahl & Loonen 1998, this volume). In all other years the pattern was rather similar, with the highest grazing pressure just after hatch and a declining grazing pressure over the rest of the summer, until the families have fledged around 20 August (Fig. 6).

Discussion

The number of barnacle geese in Kongsfjorden was estimated using three independent methods. All three methods, the Petersen estimate, the simulated population growth using total gosling production and local return rate estimates, and the census data, result in corresponding estimates with a similar pattern over time (Fig. 4). There might have been an underestimation of the population size in 1991 using a Petersen estimate because the sum of the calculated number of

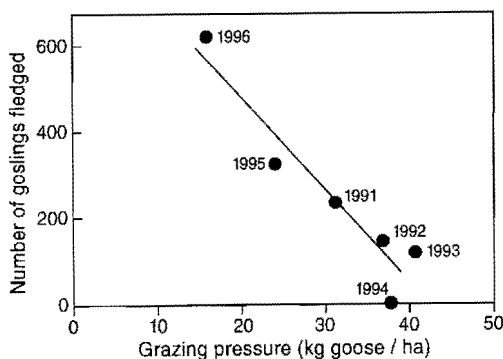


Fig. 7. A negative relation between the number of goslings produced and the grazing pressure on the mossy shore of the lake, Solvatnet ($F_{1,4} = 35.94$, $P = 0.004$). When the geese are able to use the tundra and rely less on the vegetation close to water, the total production of goslings in the colony is greater, and the goslings are heavier.

yearlings from 1990 and the number of families observed in 1991 exceed the Petersen estimate.

There is a significant variation between years in local return rate of the geese. Tombre *et al.* (1998b, this volume) showed that population size is most sensitive to changes in adult survival. Even small differences in local return rate will affect the local population growth. Local return rate is the product of survival and the proportion of living individuals which return to the natal colony. A change in survival will affect the total size of the Svalbard barnacle goose population, but a change in the proportion of living individuals returning to the natal colony only affects the distribution of the birds. However, if the probability of successful reproduction elsewhere differs, emigration might have an indirect effect on population size. A survival analysis, including sightings from the wintering grounds is necessary to discriminate between survival and local return rate and to show a density dependent effect on survival in our study colony. The sex difference in local return rate is probably caused by more males moving to other colonies than females (Anderson *et al.* 1992) as there is no indication of sex-biased mortality from the wintering grounds (J. M. Black, pers. comm.).

The continuous decline in the growth of goslings, adult size and adult body condition in the period prior and up to 1996 (Loonen *et al.* 1997) can be taken to indicate a density-dependent increase in competition for food. Gosling survival is related to gosling size (Owen

& Black 1989; Loonen *et al.* in press), and the declining trend in female gosling survival found in this study could be explained by the decline in growth rate. However, in 1996 the growth of goslings was substantial and the growth curve did not differ from the growth curve of 1991. The local presence of the arctic fox thus seemed to be a major factor affecting the growth of goslings. In the years 1996 and 1997, geese used the areas close to the village to a lesser extent and were spread out over the tundra. The absence of a predator allowed the geese to exploit the tundra vegetation without any risk of predation (Stahl & Loonen 1998, this volume). The grazing pressure on the moss vegetation along the lake shores declined, although the number of geese increased. Arctic foxes could have decreased the competition for food by killing many goslings, but the net result of their presence is an increase in competition due to a restriction of the feeding range of the geese. This effect leads to the unexpected negative relationship between the number of goslings produced and the total grazing pressure in the most important brood rearing site (Fig. 7).

Is there evidence for density dependence on gosling production in the absence of arctic foxes? A comparison between the years 1990 and 1991 against 1996 and 1997 gives very little indication for density dependence at this stage of population development. While the number of families increased from 75 to 229 (Table 2), there was hardly any change in reproductive success (Table 4). The average brood size at first sighting was 3.3 in three of the four years. The percentage of families losing all their goslings increased from 2 to 16% ($\chi^2 = 11.91$, $df = 3$, $P = 0.008$), but this trend could also have been caused by the increasing amount of data on brood sizes at hatching of the eggs. The brood size of families which successfully fledged at least one young also showed a marginal decrease from 3.1 to 3.0 goslings (Table 4). All these changes are very small compared to the threefold increase in population size.

Several authors have questioned the generality of the concept of density-dependent population regulation (reviewed in Sinclair 1989), and the recent unexpected increase in total size of the Svalbard barnacle goose population could support this doubt. However, while our study shows that density dependence on the breeding grounds exists in fox years, the variable presence of predators has a heavy effect on food availability

for the geese. If the foxes fail to reappear, there is no indication for density dependence at the present population size. However, if arctic foxes were to become permanent residents, a decline of the local population size to a lower equilibrium could be expected.

What determines the variable presence of arctic foxes? There is no clear explanation for the absence of arctic foxes in our study area in the years 1990–91 and 1996–97. Because the mainland in the Kongsfjorden area is relatively small and enclosed by glaciers, there is very little possibility for arctic foxes to migrate in and out of the area after ice breakup. Geese are migratory birds and are only potential prey from egg laying (beginning of June) to the end of wing moulting and the fledging of the goslings (end of August). Experiments with supplying food to fox dens have somewhat surprisingly failed to show that supplementary food during summer affects the reproductive output of the arctic fox (Tannerfeldt et al. 1994). Density dependence of the barnacle goose population caused by a numerical response of foxes following an increase in goose numbers is therefore unexpected.

On the European and Asian continents, arctic fox numbers are closely linked to lemming cycles, and the question whether or not the lemming cycles are caused by predation or by other factors is still not solved (Chitty 1996). In Svalbard, microtines are absent apart from one small population near a deserted mining town. Here, carcasses of reindeer and ptarmigan are the major winter food, and the numbers of arctic foxes respond to fluctuations in the availability of these items during winter (Prestrud 1992). The significance of long-distance movement of foxes over the winter ice remains an open question.

The arctic fox is the main predator of goose eggs and young in Svalbard (Madsen et al. 1992; Frafjord 1993a, b). Arctic foxes can greatly affect the reproductive output of arctic birds. The large fluctuations in the breeding success of waders and brent geese *Branta bernicla bernicla* breeding in Taimyr have been linked to the cyclic presence of large numbers of arctic foxes (Roselaar 1979; Summers 1986; Underhill et al. 1993). When foxes have access to breeding islands, almost all nests are depredated, and the reproductive output is low or absent (Madsen et al. 1992; Birkhead & Nettleship 1995; Tombre 1995).

The variable presence of arctic foxes in our study area generated fluctuations in reproductive

output and hence irregularities in population growth. The arctic fox restricted barnacle goose breeding localities to islands (Tombre et al. 1998a, this volume) and restricted moulting and brood rearing areas to the vicinity of open water (Stahl & Loonen 1998, this volume). Predation affected the number of goslings but also had indirect effects on survival during autumn migration by reducing gosling growth and adult body condition (Loonen et al. 1997). When arctic foxes are present during brood rearing, the brood rearing phase becomes an important candidate for density dependence. Without arctic foxes present in the area, geese escape from density dependence at present density.

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