Critical components in the dynamics of a barnacle goose colony: A sensitivity analysis

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The considerable increase in arctic goose populations over the last decades has induced large ecological and economical impacts on the environment. When planning how to alleviate some of these problems, environmental managers will need background information on the behaviour and dynamics of arctic goose populations. In this study the demographic parameters which have the strongest effect on population growth are assessed. Sensitivity/elasticity analyses were performed on an eight-year data set of a newly established barnacle goose *Branta leucopsis* colony in Kongsfjorden, Svalbard. The work included measurement of the sensitivity of the population's growth rate to changes in different demographic parameters and of how relative changes in different demographic parameters influence relative changes in population growth rate (elasticity analysis). An evaluation was made of which demographic parameters were most responsible for the variation in population growth the last eight years. The results from these analyses demonstrated that adult survival rates and late gosling survival were the most important factors determining changes in the colony's growth rate, followed by early gosling and egg survival. Juvenile survival rates had less effect on the population growth rate, whereas clutch size had the least effect. Results from the elasticity analyses showed that a proportional change in adult survival rates will have an impact on the growth rate 2.1 times greater than a proportional change in any of the other demographic parameters measured. During the last eight years, juvenile return rate, gosling summer survival and clutch size had been responsible for most of the variation in the growth rate of the colony. The variation was closely correlated to the presence of arctic foxes in the area. Body reserves are important for successful migration, and a reduction in adult survival rates due to insufficient reserves could cause the barnacle goose colony in Kongsfjorden to decrease rapidly. In addition to the high sensitivity of adult survival rates, the high sensitivity of gosling survival during the brood rearing period further illustrates the importance of securing good feeding habitats prior migration.

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Introduction

Several European and North American arctic goose populations have increased considerably during the last decades (Owen 1982, 1984; Owen & Black 1989; Ebbinge 1992; Cooke et al. 1995). As a consequence, their impact has induced large ecological and economical problems on the environment (Ankney 1996). Conflicts with farmers in the winter and spring staging areas have increased with the increasing numbers of geese (e.g. Roomen & Madsen 1993). In La Pérouse Bay, the breeding habitats for snow geese *Anser caerulescens caerulescens* have been seriously degraded due to overgrazing (Williams et al. 1993; Cooke et al. 1995). Other arctic goose populations, however, do not seem to follow this increasing trend, the reasons for which are presently unclear (light-bellied brent goose *Branta bernicla hrota* in Svalbard: Madsen et al. 1989; emperor goose *Chen canagica* in Alaska: Schmutz et al. 1997).

Depending on the policy and the desired results, the management and conservation of arctic goose populations usually involve action plans in order to maintain or increase the current number of

geese. A certain amount of knowledge about the population in question is necessary before such plans can be put in operation (Black 1998). When studying changes in population size, it is necessary to determine which demographic parameters have the strongest effect on the population's growth rate. Summer and winter survival of both adults and juveniles and several reproduction parameters all have potential impacts on population size (e.g. Schmutz et al. 1997). Several studies on different bird species have provided this type of information which has been used as a basis for conservation recommendations for managers (e.g. Florida scrub jay *Aphelocoma c. coerulescens*: Woolfenden & Fitzpatrick 1991; Hawaiian geese *Branta sandvicensis*: Black & Banko 1994, Black 1995; willow grouse *Lagopus lagopus*: Steen & Erikstad 1996; emperor goose: Schmutz et al. 1997).

There are several approaches to studying changes in population size. A sensitivity analysis (Caswell 1989), which is an unscaled measure of the impact of a parameter, measures how the growth rate changes when one of the demographic parameters changes. The elasticity approach, however, allows a direct comparison between variables (de Kroon et al. 1986). When the values are standardised in relative units, the isolated effects of each parameter can be compared directly and the influence of proportional changes in different demographic parameters on growth rate can be measured. In order to evaluate which demographic parameters have been responsible for the actual observed variation in growth rate, the between year coefficient of variation (CV) for each parameter can be multiplied with the corresponding elasticity coefficient. We then obtain an estimate which demonstrates the actual effect of a parameter on the population's growth rate, the Actual-Elasticity coefficient (the AE-coefficient, van Tienderen 1995, see also Steen & Erikstad 1996). All three of these approaches investigate the critical components in the dynamics of a population and are very useful for managers in identifying the key demographic parameters for future population management programs.

The Svalbard population of the barnacle goose *Branta leucopsis* has increased steadily over the last fifty years (Owen 1984; Owen & Black 1989; Black 1998). The population has increased stepwise, presumably due to the fact that new areas in Svalbard are being occupied by newly establishing colonies (Black 1998). Some of the colonies show signs of density-dependent effects through decreased productivity, survival, growth rates and final body size (Black 1998; Loonen et al. 1997; Drent et al. 1998, this volume). However, we still lack a complete understanding of the factors determining the dynamics in this population (see Pettifor et al. 1998, this volume).

The barnacle goose colony in Kongsfjorden, near the village of Ny-Ålesund on the western coast of Svalbard, is a fairly new colony with the first breeding pair recorded in 1980 (Tombre et al., this volume) The colony has been monitored since then, and after 1989 more intensive studies have been carried out, both descriptive and experimental (Alsos 1995; Bishop et al. 1995; Black et al. 1996; Tombre 1995; Tombre & Erikstad 1996; Tombre et al. 1996; Dalhaug et al. 1996; Loonen 1997; Loonen et al. 1998, this volume). The colony has increased today numbers almost 800 individuals (Loonen et al. 1998, this volume).

In this study sensitivity/elasticity analyses were performed to evaluate which demographic factors have the strongest effect on the growth rate of the Kongsfjorden colony. Several demographic parameters, reproduction parameters and juvenile and adult survival estimates from 1990–1997 were used. The AE-coefficients were also estimated for the same parameters. From the results of this study, the potentially most influential parameters which affect the growth rate of this colony can be identified (sensitivity/elasticity analyses), and the parameters which have actually been responsible for the variation in the colony growth the last eight years can be identified (AE-coefficients). The parameters can thus be ranked according to the amount of variation they have been responsible for. The identification of key management factors will provide information needed for planning conservation and management strategies for the Svalbard barnacle goose population as a whole.

The species studied and study area

The Svalbard barnacle goose population spends the winter on the Solway Firth, in the United Kingdom. Before the geese arrive at the breeding areas in Svalbard in May, they spend approximately one month on their traditional spring staging area in the Helgeland archipelago on the

coast in middle Norway (Gullestad et al. 1984; Black et al. 1991; Black & Owen 1995) and some weeks staging in Svalbard as well (Tombre et al. 1996). The geese in Kongsfjorden (78°55′N, 12°15′E) arrive at their breeding areas in late May and early June (Tombre et al. 1996). The majority of the pairs start nesting after only a few days, but some delay nesting for one or two weeks (Dalhaug et al. 1996; unpubl. data). The barnacle goose is a determinant layer with a single clutch of 2–6 eggs. Every year some pairs nest on the mainland close to Ny-Ålesund (2–10 pairs), but the majority of the nests are found on the islands in Kongsfjorden near Ny-Ålesund (Tombre et al., this volume). In years of unfavourable sea-ice conditions, that is, if the ice still connects the islands to the mainland when egg laying starts, arctic foxes *Alopex lagopus* prey heavily on goose eggs (Tombre 1995). During the incubation period, eggs may also be preyed upon by glaucous gulls *Larus hyperboreus* and arctic skuas *Stercorarius parasiticus*, but no egg predation has been observed when the female is on the nest (unpubl. data). After hatching, the parents bring their young across the fjord to the mainland, and the areas around Ny-Ålesund are important brood rearing sites for most goose families in the colony. During this period, goose families may suffer great losses of goslings in years with arctic foxes in the area. In years when foxes are present, families are forced to feed on the moss vegetation close to the water edges of the lakes. Without foxes, however, families are more dispersed and feed on the tundra (Loonen et al. 1998, this volume). The families stay in the Kongsfjorden area until wing moult is completed. The more than 3,000 km migration back to the U.K., a flight mostly over sea, is one of the most demanding events in the lifetime of the Svalbard barnacle goose (Owen 1982; Owen & Gullestad 1984).

Today, more than 70% of the adults in the Kongsfjorden colony are individually marked with coded, plastic leg bands and metal rings. Rings are readable with a telescope at a distance of up to 250 m (for details in the ringing procedures see Owen & Black 1989; Black & Owen 1995; Loonen et al. 1998, this volume).

Methods

From 1990 to 1997, rings were recorded as the geese arrived in the Kongsfjorden area. By daily visits to the two main breeding islands, Storholmen (30 ha, 6 km from Ny-Ålesund, average 114 nests 1992–1997) and Prins Heinrichøya (3 ha, 1 km from Ny-Ålesund, average 24 nests 1992–1997), the following reproductive parameters were recorded: *Clutch size* – number of eggs laid per female, excluding nests with only one egg; *Egg survival* – the fraction of eggs surviving to hatching. After hatching, when the majority of the families were feeding in the areas around Ny-Ålesund, family size and gosling survival in the brood rearing period were recorded by daily observations. In this period, data for the following parameters were collected: *Early gosling survival* – the observed proportion of goslings surviving from hatching to day 10 after peak hatch; *Late gosling survival* – the observed proportion of goslings surviving from day 10 after peak hatch until day 30 after peak hatch. In 1990 and 1991, data on brood size at hatching and early family size are limited and therefore not used in the analyses. Neither are there any reproductive parameters or juvenile survival estimates for 1994 since arctic foxes took all the eggs on the main breeding islands due to late breakup of sea-ice (see above).

Survival estimates were based on sightings of ringed geese in the two following seasons. For juveniles, survival estimates were made for females only since female juveniles have a higher return rate to the colony than male juveniles (Loonen 1997). Juveniles do not breed in their first summer, and they move around in the area more frequently than breeding adults. Accordingly, some juveniles are not seen in Kongsfjorden before their second summer and good survival estimates for juveniles are therefore lacking in 1996. For adult females, survival estimates in 1996 were based on one year only. The following survival estimates were calculated: *Juvenile autumn survival rate* – number of ringed juvenile females surviving to the wintering area divided by the number of ringed juvenile females (goslings) in Kongsfjorden; *Juvenile return rate* – number of ringed juvenile females returning to Kongsfjorden divided by the number of ringed juvenile females surviving to the wintering area; *Adult autumn survival rate* – number of ringed adult females surviving to the wintering area divided by the number of ringed adult females in Kongsfjorden; *Adult return rate* – number of ringed adult females returning to Kongsfjorden divided by the number of ringed adult females surviving to the wintering area.

Weighted mean values (which account for different sample sizes in different years) were calculated for the eight demographic parameters listed above. The population growth of the colony was modelled as the change in the number of adult females present in the colony (N_t) from one year to another (N_{t+1}):

$$N_{t+1} = A \times N_t$$

using a Leslie matrix (Caswell 1989) with three age classes; 0–1 year, 1–2 years and 2+ years. When the geese have survived their first year, survival rates are assumed to be similar for all age-classes (Owen & Black 1989).

The yearly survival and reproduction parameters are defined as:

Adult survival = adult autumn survival × adult return rate,

Juvenile survival = juvenile autumn survival × juvenile return rate,

Reproduction rate = (clutch size × 0.5) × egg survival × early gosling survival × late gosling survival.

The long-term population growth rate, λ, is the dominant eigenvalue of the Leslie matrix A (Caswell 1989). The sensitivity for a demographic parameter X_i on the growth rate, λ, is defined by

$$S_i = \partial\lambda/\partial X_i$$

The sensitivity for the overall adult survival is therefore

$$\partial\lambda/\partial S_{Adult} = \partial\lambda/\partial S_{Ad.autumn} \times \partial S_{Ad.autumn}/\partial S_{Adult}$$

where S_{Adult} = Adult survival and $S_{Ad.autumn}$ = adult autumn survival. Correspondingly, the sensitivity of adult autumn survival is

$$\partial\lambda/\partial S_{Ad.autumn} = \partial\lambda/\partial S_{Adult} \times \partial S_{Adult}/\partial S_{Ad.autumn}$$

In all analyses, we assume that all demographic parameters are independent and that the sex ratio at hatching is 50:50. By definition (de Kroon et al. 1986), the elasticity coefficient, E_i, to the parameter X_i is:

$$E_{Xi} = \partial\log\lambda/\partial\log X_i = X_i/\lambda \times \partial\lambda/\partial X_i$$

The variables comprising overall adult survival, overall juvenile survival or reproduction, will all have similar elasticities. For adult survival, this can be seen from the expression

$$\begin{aligned} E_{SAd.autumn} &= \partial\log\lambda/\partial\log S_{Ad.autumn} \\ &= S_{Ad.autumn}/\lambda \times \partial\lambda/\partial S_{Ad.autumn} \\ &= S_{Ad.autumn}/\lambda \times \partial\lambda/\partial S_{Adult} \times S_{Ad.return} \\ &= S_{Adult}/\lambda \times \partial\lambda/\partial S_{Adult} = E_{SAdult} \end{aligned}$$

where $S_{Ad.return}$ = adult return rate. The AE-coefficients were calculated following Steen & Erikstad (1996):

$$AE\text{-coefficient} = CV_i \times E_i$$

where CV_i is the coefficient of variation for parameter i and E_i is the elasticity of i with respect to λ. The CV for each demographic parameter is calculated by dividing the standard deviation for that parameter by the corresponding weighted mean value.

Results

The geese laid around three or four eggs in all years. In 1994, no clutches survived due to fox predation. Few eggs were lost during incubation (mean egg survival rate = 0.88), but as summer progressed gosling losses increased (Table 1). Approximately 75% of the juveniles survived from autumn to the following spring, whereas the mean estimates of adult survival rates were approximately 90% (Table 1).

The colony of barnacle geese has increased rapidly during the last eight years, and the estimated growth rate, λ, based on the previous Leslie matrix, was 1.1599 in this period. Sensitivity values are shown in Table 2, and the parameters are listed with decreasing sensitivity indices. Adult survival rates and late gosling survival are the most important factors determining changes in the colony's growth rate. The sensitivity indices for early gosling and egg survival were somewhat smaller, followed by juvenile survival rates. Clutch size had the smallest influence on λ (Table 2).

The reproduction parameters had almost similar elasticity with respect to λ as the juvenile survival rates (Table 3). The elasticity of adult autumn survival and adult return rate had the largest impact on growth rate, and a proportional change in any of the adult survival estimates will influence growth rate 2.1 times greater than a proportional change in any of the other demographic traits.

The CV varied considerably between demo-

Table 1. Reproduction parameters, juvenile and adult survival estimates measured for barnacle geese in Kongsfjorden, Svalbard, 1990–1997. See methods for parameter definitions. The table gives mean values per year, sample sizes in parentheses.

Year	Clutch size	Egg survival	Early gosling survival	Late gosling survival	Juvenile gosling survival	Juvenile autumn rate	Adult return survival	Adult autumn rate
1990	3.74 (27)	*	*	0.94 (94)	*	*	0.98 (100)	0.94 (94)
1991	4.06 (18)	*	*	0.96 (46)	0.96 (76)	0.87 (66)	0.96 (208)	0.92 (191)
1992	3.44 (112)	0.81 (75)	0.95 (61)	0.60 (61)	0.69 (36)	0.47 (17)	0.99 (384)	0.87 (334)
1993	3.30 (212)	0.92 (171)	0.69 (71)	0.51 (71)	0.62 (21)	0.52 (11)	0.92 (440)	0.84 (368)
1994	0	*	*	*	*	*	0.91 (442)	0.86 (382)
1995	3.89 (94)	0.84 (94)	0.72 (94)	0.65 (94)	0.64 (45)	0.62 (28)	0.91 (425)	0.88 (373)
1996	3.93 (112)	0.90 (80)	0.82 (80)	0.94 (128)	*	*	0.71 (403)	0.83 (336)
1997	3.73 (153)	0.87 (146)	0.95 (66)	0.85 (66)	*	*	*	*
Weighted mean:	3.62	0.88	0.81	0.76	0.78	0.73	0.90	0.87
SD:	1.34	0.04	0.12	0.33	0.16	1.18	0.09	0.04

graphic parameters (Table 3). A high CV also implies a high AE-coefficient, demonstrating a high variance in the trait. Each parameter was ranked for sensitivity according to their AE-coefficients. Juvenile return rate, late gosling survival and clutch size showed most variation during the period 1990–1997, and the AE-coefficients indicated that these parameters were the most important factors responsible for the variation in growth rate of the colony over the last eight years. Egg survival, adult return rate and early gosling survival, however, showed less variation and had the smallest impact on the variation in growth rate in the colony. Adult and juvenile autumn survival had intermediate values.

Discussion

The potential growth rate of the barnacle goose colony in Kongsfjorden was not sensitive to variations in clutch size. The production of few eggs or the loss of eggs to predators will have a negligible effect on the total growth rate of the colony (Table 2). However, in years with delayed breakup of sea ice, foxes can deplete the whole area for eggs and thereby prevent the production of recruits that year. Such years contribute considerably to the variation in growth rate in the colony

(Table 3). The amount of sea ice and the time of breakup in Kongsfjorden varies considerably between years (Parker & Mehlum 1991), and during its lifetime a barnacle goose may experience several breeding seasons with total nest failure due to fox predation (Tombre 1995). In colonies where geese nest on islands which in some years are exposed to foxes during egg laying and incubation, loss of eggs to predators may strongly influence the breeding success of the colony. This also affects the variation in growth rate as a whole. Arctic foxes also have an impact on the yearly production in brent geese *Branta b. bernicla* in Taimyr (B. Ebbinge pers. comm.). Brent geese nesting on the mainland suffer high egg losses in years when foxes are present. In years with late breakup of ice-bridges, geese nesting on islands are also exposed to foxes. Accordingly, the yearly production of young strongly and negatively highly correlates with the presence of foxes.

With respect to egg survival, the sensitivity of the Kongsfjorden colony's growth rate was intermediate, and a variation in egg survival will have a small effect on the growth rate of the population (Table 2). During incubation, few eggs were lost and the variation in losses between years was small, giving egg survival the smallest AE-coefficient in Table 3. Egg survival is therefore the parameter least responsible for the variation in growth rate in the Kongsfjorden colony.

After the young are hatched, the parents take their young across the fjord to the mainland, a

Table 2. Ranked sensitivity for eight demographic parameters (see methods for definitions) in a colony of barnacle geese in Kongsfjorden, Svalbard, 1990–1997. See methods for calculations of sensitivities.

Demographic parameter	Sensitivity
Adult return rate	0.6793
Late gosling survival	0.6573
Adult autumn survival	0.6567
Early gosling survival	0.6168
Egg survival	0.5677
Juvenile return rate	0.2834
Juvenile autumn survival	0.2652
Clutch size	0.1380
Adult survival	0.7548
Reproduction rate*	0.5095
Juvenile survival	0.3633

* clutch size, egg survival, early and late gosling survival.

1–6 km long journey depending on which island the geese nest. Goslings are subject to predation by glaucous gulls and arctic skuas during this phase. Later, in the brood rearing period on the mainland, arctic foxes are the main predator. In 1990–1991 and 1996–1997 no foxes were recorded in Kongsfjorden, and the effect of fox predation on late gosling survival is demonstrated in Table 1. In years without foxes, late-gosling survival was high (between 85% and 96%). On the other hand, in years when foxes were present (1992–1995), the predation on goslings was considerable (gosling survival between 51% and 65% and no surviving goslings in the extreme year 1994). In such years, goose families keep to safe feeding areas near the lakes and evidence of density dependent effects on gosling growth rate and gosling survival have been reported (Loonen et al. 1997, 1998, this volume). Accordingly, gosling survival during the brood rearing period has probably been one of the main components determining the variation in growth rate the last eight years (Table 3), and the presence of foxes seem to play a major role for the dynamics within the colony. There are no small rodents in Svalbard, except for a very localised population 100 km south (Yoccoz et al. 1993), so the presence of foxes is not related to cyclic variations in density of prey as in Taimyr. It is not clear why foxes have been totally absent in Kongsfjorden the last few years (E. Fuglei pers. comm.), and a better understanding of fox dynamics would increase our

chances of predicting changes in colony size of barnacle geese at a local level.

The variation in juvenile return rate was considerable, and this parameter also seems to have played a major role in the variation in growth rate (ranked with the highest AE-coefficient in Table 3). The variation in return rate may be due to variable winter conditions on the Solway Firth in the U.K., where severe winters may influence the first-year survival. Another possibility, however, is that yearlings disperse to new breeding colonies. There has been a significant decline in local return rate during recent years, both for female adults and female juveniles (Loonen et al. 1998, this volume). However, Table 1 only includes data from five years (and one year was anomalous), and data from additional years are needed in order to evaluate the significance of juvenile return rate on the future size of the Kongsfjorden colony.

In addition to gosling survival in the brood rearing period, adult survival was the most profound determining component for changes in growth rate of the Kongsfjorden colony (Table 2). A small change in adult autumn survival rate or adult return rate will strongly influence changes in population size. A proportional change in any of the adult survival estimates will have an impact on growth rate 2.1 times greater than a proportional change in any other demographic parameter (Table 3). In an individual-based population model for emperor geese, Schmutz et al. (1997) also found that altering adult survival had a considerable effect on the population growth rate compared to equally proportionate changes in either juvenile survival or reproductive parameters. Table 1 shows that adult survival rates have been high and stable, and Table 3 demonstrates that the adult survival parameters' contribution to the variation in growth rate has been negligible (lowest rank on the elasticity' list). We should note that survival estimates in 1996 were based on one year only, giving a smaller mean value in this year than in previous years and thereby increasing the standard deviation value (Table 1). In the wintering area, the entire Svalbard population gathers in a concentrated area and two years of sightings are needed in order to give a good estimate of autumn survival. The low value for 1996 therefore influences the variation in the autumn survival parameters, giving adult autumn survival a higher rank on the AE-coefficient list than what we might expect (Table 3).

The high sensitivity indices for adult survival

Table 3. Ranked elasticity coefficients, coefficient of variation (CV) and actual elasticity coefficients (AE-coefficients) for eight demographic parameters in a colony of barnacle geese in Kongsfjorden, Svalbard, 1990–1997. The CV-values are calculated from weighted standard deviations and weighted mean values in Table 1.

Demographic parameter	Elasticity	CV	AE-coeff.	Ranking from sensitivity
Juvenile return rate	0.2452	1.616	0.396	1
Juvenile autumn survival	0.2452	0.205	0.050	5
Clutch size	0.2453	0.370	0.091	3
Egg survival	0.2453	0.045	0.011	8
Late gosling survival	0.2453	0.434	0.106	2
Early gosling survival	0.2453	0.148	0.036	6
Adult autumn survival	0.5095	0.100	0.051	4
Adult return rate	0.5095	0.046	0.023	7

rates support the predicted response for long-lived species, where a small reduction in adult survival rate will have a large negative impact on the number of expected future breeding attempts (Charlesworth 1980; Wooller et al. 1992). Accordingly, long-lived species should not sacrifice their own survival and future fecundity for investment in the current offspring (Lindén & Møller 1989) but instead shunt increased reproductive costs to their offspring (Mauck & Grubb 1995). In years with poor breeding conditions, we therefore expect parents to reduce their parental effort and maximise adult survival rates (Erikstad et al. 1998). Accordingly, regardless of variable breeding conditions, we expect the adult survival rate to remain high because a small change in survival rates potentially has strong effects on the population growth rate.

Successful management measures, such as protecting the Svalbard barnacle geese from hunting and the establishing of reserves on both wintering and breeding grounds in Svalbard (Owen 1984), have resulted in an increase of numbers from a count of approximately 300 individuals in 1948 (Owen & Black 1989) to the current estimated number of 23,000 individuals (Black 1998). This population increase may also be partly due to the shifting of habitat use, where the geese depend increasingly on agricultural land (e.g. Black et al. 1991).

According to the results from this study, which also are supported by general life-history theory (e.g. Stearns' 1992), a small decrease in adult survival rates could cause the Kongsfjorden colony to decrease rapidly. If the hunting of barnacle geese is reintroduced, the whole population could rapidly decrease. However, even if the

species continues to be protected, good feeding habitats must be secured prior to migration to enable the geese to build up body reserves necessary for successfully completing migration (Owen & Black 1989). The barnacle goose species has a high adult survival rate and a relatively high reproductive potential, i.e. it produces relatively large clutch sizes. Such species commonly live in favourable breeding and survival habitats, but the annual variation in breeding habitats is usually large (Sæther et al. 1996). For these so-called bet-hedging species, it is important from a management point of view to secure not only good winter/survival habitats but also good summer/breeding habitats. For migratory species, feeding conditions prior to migration are especially important if the adults have problems gaining enough body reserves to survive autumn or spring migration; a decreased adult survival rate could mean a rapid decrease in the population. The high sensitivity of gosling survival in the brood rearing period also demonstrates the importance of securing good feeding habitats for goslings before the start of autumn migration. However, the influence of feeding conditions on gosling survival will strongly be determined by the fox dynamics in the area.

References

Alsos, I. G. 1995: The relationship between nest site, diet and behaviour in barnacle geese *Branta leucopsis* in Kongsfjorden, Svalbard. Cand. Scient. Thesis, Univ. i Tromsø.

Ankney, C. D. 1996: An embarrassment of riches: too many geese. *J. Wildl. Manage. 60(2)*, 217–223.

Bishop, C. M., Butler, P. J. Egginton, S., El Haj, A. J. & Gabrielsen, G. W. 1995: Development of metabolic enzyme activity in locomotor and cardiac muscles of the migratory barnacle goose. *Am. J. Physiol. 269*, R64–R72.

Black, J. M. 1995: The Nene recovery initiative: research against extinction. *Ibis 137*, 153–160.

Black, J. M. 1998: Conservation and management plan for the Svalbard population of Barnacle Geese. Prepared for the Directorate for Nature Management and Scottish Natural Heritage. *DN-Rapport 1998/2*, 1–111.

Black, J. M. & Banko, P. C. 1994: Is the Hawaiian Goose saved from extinction? Pp. 394–410 in Olney, P. J., Mace G. & Feistner, A. (eds.) *Creative conservation: interactive management of wild and captive animals.* Chapman & Hall, London.

Black, J. M. & Owen, M. 1995: Reproductive performance and assortative pairing in relation to age in barnacle geese. *J. Anim. Ecol. 64*, 234–244.

Black, J. M., Deerenberg, C. & Owen, M. 1991: Foraging behaviour and site selection of barnacle geese *Branta leucopsis* in a traditional and newly colonised spring staging habitat. *Ardea 79*, 349–358.

Black, J. M., Choudhury, S. & Owen, M. 1996: Do geese benefit from life-long monogamy? Pp. 91–117 in Black, J. M. (ed): *Partnership in birds. The study of monogamy.* Oxford University Press, Oxford.

Caswell, H. 1989: *Matrix Population Models, Analysis, and Interpretation.* Sinauer Associates, USA. 328 pp.

Charlesworth, B. 1980: *Evolution in Age-Structured Populations.* Cambridge University Press, Cambridge.

Cooke, F. G., Rockwell, R. F. & Lank, D. B. 1995: *The Snow Geese of La Pérouse Bay, Natural Selection in the Wild.* Oxford University Press.

Dalhaug, L., Tombre, I. M. & Erikstad, K. E. 1996: Seasonal decline in clutch size of the Barnacle Goose in Svalbard. *Condor 98*, 42–47.

de Kroon, H., Plaisier, A., Van Groenendael, J. & Caswell, H. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology 67*, 1427–1431.

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 Polarinst. Skr. 200*, this volume.

Ebbinge, B. S. 1992: Population Limitation in Arctic-breeding Geese. *Doctoral dissertation, Univ. Groningen, The Netherlands.*

Erikstad, K. E., Fauchald, P., Tveraa, T. & Steen, H. 1998: On the cost of reproduction in long-lived birds; the influence of environmental variability. *Ecology 79(5)*, 1781–1788.

Gullestad, N., Owen, M. & Nugent, M. J. 1984: Numbers and distribution of Barnacle Geese *Branta leucopsis* on Norwegian staging islands and the importance of the staging area to the Svalbard population. *Norsk. Polarinst. Skr. 181*, 57–65.

Linden, M. & Møller, A. P. 1989: Cost of Reproduction and Covariation of Life History Traits in Birds. *TREE 4*, 367–371.

Loonen, M. J. J. E. 1997: Goose breeding ecology: overcoming successive hurdles to raise goslings. Ph.D. thesis, University of Groningen.

Loonen, M. J. J. E., Oosterbeek, K. & Drent, R. H. 1997: Variation in growth and adult size: evidence for density dependence. *Ardea 85(2)*, 177–192.

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 Polarinst. Skr. 200*, this volume.

Madsen, J., Bregnballe, T. & Mehlum, F. 1989: Study of the breeding biology and behaviour of the Svalbard population of Light-bellied Brent Goose *Branta bernicla hrota. Polar Res. 7*, 1–21.

Mauck, R. A. & Grubb, T. C., Jr. 1995: Petrel parents shunt all experimentally increased reproductive costs to their offspring. *Anim. Behav. 49*, 999–1008.

Owen, M. 1982: Population dynamics of Svalbard barnacle geese, 1970–1980. The rate, pattern and causes of mortality as determined by individual marking. *Aquila 89*, 229–247.

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*, 603–617.

Owen, M. & Gullestad, N. 1984: Migration routes of Svalbard Barnacle Geese *Branta leucopsis* with a preliminary report on the importance of the Bjørnøya staging area. *Norsk Polarinst. Skr. 181*, 67–77.

Parker, H. & Mehlum, F. 1991: Breeding population size of the Common Eider *Somateria mollissima* in Kongsfjord, Svalbard, 1981–1987. *Norsk Polarinst. Skr. 195*, 21–29.

Pettifor, R., Black, J. M., Owen, M., Rowcliffe, J. M. & Patterson, D. 1998: Growth of the Svalbard barnacle goose *Branta leucopsis* winter population 1958–1996: An initial review of temporal demographic changes. Pp. 147–164 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 Polarinst. Skr. 200*, this volume.

Roomen, M. van & Madsen, J. 1993: Waterfowl and agriculture: Review and future perspective on the crop damage conflict in Europe. Proceedings of the international workshop 'Farmers and waterfowl: Conflict or Coexistence', Lelystad, The Netherlands, 6–9 October 1991. *IWRB Special Publication No. 21*, 1–183.

Schmutz, J. A., Rockwell, R. F. & Petersen, M. R. 1997: Relative effects of survival and reproduction on the population dynamics of emperor geese. *J. Wildl. Manage. 61*, 191–201.

Stearns, S. C. 1992: *The Evolution of Life Histories*. Oxford University Press, Oxford.

Steen, H. & Erikstad, K. E. 1996: Sensitivity of willow grouse *Lagopus lagopus* population dynamics to variations in demographic parameters. *Wildlife Biol. 2*, 27–35.

Sæther, B.-E., Ringsby, T. H. & Røskaft, E. 1996: Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos 77*, 217–226.

Tombre, I. M. 1995: Reproductive effort in high-arctic barnacle geese; the importance of body mass and the date of egg laying. Dr.scient.thesis, University of Tromsø.

Tombre, I. M. & Erikstad, K. E. 1996: An experimental study of incubation effort in high-arctic barnacle geese. *J. Anim. Ecol. 65*, 325–331.

Tombre, I. M., Erikstad, K. E., Gabrielsen, G. W., Strann, K. B. & Black, J. M. 1996: Body condition and spring migration in high-arctic barnacle geese. *Wildl. Biol. 2*, 247–251.

Tombre, I. M., Mehlum, F. & Loonen, M. J. J. E. 1998. The Kongsfjorden colony of barnacle geese: Nest distribution and the use of breeding islands, 1980–1997. Pp. 57–65 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 Polarinst. Skr. 200*, this volume.

van Tienderen, P. H. 1995: Life cycle trade-offs in matrix population models. *Ecology 76*, 2482–2489.

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. i*, 766–777.

Woolfenden, G. E. & Fitzpatrick, J. M. 1991: Florida scrub jay ecology and conservation. Pp. 542–565 in Perrins, C. M., Lebreton, J.-D. & Hirons, G. J. M. (eds.): *Bird Population Studies, relevance to conservation and management*. Oxford University Press. Oxford.

Wooller, R. D., Bradley, J. S. & Croxall, J. P. 1992: Long-term population studies of seabirds. *TREE 7*, 111–114.

Yoccoz, N. G., Ims, R. A. & Steen, H. 1993. Growth and reproduction in island and mainland populations of the vole *Microtus epiroticus. Can. J. of Zool. 71*, 2518–2527.