

Geese and their future fortune

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Wild goose populations were probably limited by winter food supplies before Man modified their winter range and effectively removed that limitation on population growth. At the same time, reduction of hunting lowered Man-induced mortality and allowed most populations to increase both in Europe and in North America.

This paper considers likely future trends, and, using the population of Barnacle Geese breeding in Svalbard as an example, suggests how numbers might be regulated in a density-related manner. The Svalbard Barnacle Goose population has shown a decline in recruitment rate and an increase in the natural mortality rate as numbers have increased. Both of these are reflections of competition on the breeding grounds, though there may be some effects at other times. We suggest that most populations will eventually be limited by resources on the breeding area.

Some of the implications of changes in numbers are that pair-bond stability and breeding area philopatry are less advantageous and in time will become less pronounced as the selective value of these traits are diminished.

We argue that both for applied reasons (conservation, crop damage prediction) and for academic investigations of population processes, long-term studies are vital in the management and understanding of goose populations. A number of features of their life history make geese very suitable subjects for such studies.

Wild goose populations are among the most frequently counted and individually marked of any birds. Because of their interest as shooting quarry and because of international agreements on conserving migratory species, their numbers and breeding success have been assessed on a long-term basis. Most of the studies of population dynamics in geese have been carried out by potential exploiters and conservation managers, with the aim of maximizing harvests or predicting future population trends. By changing shooting pressure or patterns, goose populations in North America and Eurasia have been managed, often around arbitrarily set 'target' population sizes (see e.g. Gauvin & Reed 1987).

Studies of population dynamics depend on assessing recruitment, mortality, immigration and emigration. Geese have a number of advantages over other birds for the study of population processes:

- (a) many species occur in rather small, effectively closed, populations, so that immigration and emigration can effectively be discounted;
- (b) geese are traditional birds with well-defined and often restricted ranges;
- (c) the juveniles and adults of most species can be distinguished in the field in winter so that recruitment can be measured directly;

- (d) geese become flightless for 4-5 weeks in summer and can be rounded up in large numbers for marking. Marked individuals can be identified at long range.

Long-term studies of geese are valuable in order to safeguard populations; trends in numbers, recruitment and mortality in relation to environmental factors can indicate crucial times during the life cycle where a particular resource may be limiting and lead to prediction of future population sizes. These predictions are increasingly called for by agricultural, shooting and conservation interests as more species come into conflict with farmers and as some begin to approach the limit of the carrying capacity of their Arctic summering areas (Owen 1990). The birds can also be used as biological indicators of the health of the environment, particularly the productivity of Arctic breeding areas.

Long-term studies are crucial to the understanding of the processes involved in evolutionary change. Examining the lifetime reproductive success is a particularly useful way of understanding the importance of particular life history strategies (see e.g. Newton 1989a). Geese are long-lived, with a maximum lifespan in excess of 25 years, so studies of lifetime production are of necessity long-term.

This paper summarizes the changes in numbers of European goose species in relation to changes in conditions on the

wintering grounds, and examines evidence for density-dependent processes that might lead to limits on population growth in future. We look in more detail at the population of Barnacle Geese *Branta leucopsis* which breeds in Svalbard and winters in northern Britain, for clues as to future population limitation and the effect of changes in population size on the selective advantages of some of the birds' life history traits.

BACKGROUND

Geese are generally Arctic breeders, undergoing long migrations to winter in temperate zones. They have developed a range of feeding apparatus adapted to exploit different habitats and foods in winter. In summer all species feed by grazing tundra vegetation and in some areas a number of species occur together using the same nesting and rearing areas. This and the probable extent of the historical wintering range and the present breeding areas mean that before Man so modified temperate habitats, goose populations were probably limited by winter food both in Europe (Owen 1976) and in North America (C. D. MacInnes in Owen 1980). There are a few examples from historical times of large die-offs in relation to food shortage, especially in periods of severe weather (see e.g. Rogers 1979).

RECENT CHANGES IN NUMBERS

The trends in numbers of goose populations wintering in Europe are shown in Table 1, together with indications of changes in hunting pressure. There is a considerable amount of evidence that it was the hunting mortality that was

keeping the number of many species in check in the past (Ebbing 1990). In North America, restriction and relaxation of shooting of Canada Geese *Branta canadensis* were closely reflected in changes in population size (Reeves *et al.* 1968). Harvests of Atlantic Brant *Branta bernicla hrota* in the 1960s and 70s were largely responsible for the changes in numbers of that population (Rogers 1979). Similarly, Ebbing (1990) has demonstrated that the restriction of shooting of a number of populations of geese wintering in Europe led to corresponding changes in mortality which were reflected in changes in population size. Thus, in goose populations the mortality imposed by shooting, at current population levels, is additive and there is little evidence of density-dependent processes coming into play, despite the fact that many populations have increased in size three- or more-fold in the last three decades.

If numbers in the past were limited in winter, either by food shortage or hunting, it is not surprising that changes in one or both of these factors will result in changes in numbers. The breeding areas of most species remain largely unaffected by Man, but their winter range has been drastically changed. Large areas of open land have been created and, at present population sizes, winter food is effectively unlimited. Mortality from shooting has been greatly reduced, either by complete protection of species (only four of the eight subspecies of geese wintering in Europe can now legally be hunted), or by changes in the practices of hunters (sometimes led by legislation such as that which banned the sale of dead wild geese in Britain in 1967) and the creation of non-shooting reserves (see Table 1).

Recent analyses have shown that weather conditions on spring staging areas and on the breeding range are correlated with recruitment rate and the population size of Pink-footed *Anser brachyrhynchus* and Greylag Geese *A. anser* breeding in

Table 1. The increases in numbers of geese wintering in Europe and an indication of changes which may have been responsible. Increases are represented as multiples of population levels in the early 1960s, when accurate counting began. *References:* 1. Rooth *et al.* (1981); 2. Madsen (1987); 3. Fox *et al.* (1989); 4. Owen & Black (1989a); 5. Ebbing (1990); 6. Fox & Gitay (1990); 7. Wilson *et al.* (1991).

Population	Breeding area	Increase since 1960s	Hunting pressure change	Reference
<i>Anser fabalis</i>	Siberia	× 6	? reduced	1
	Scandinavia/Siberia	× 2.5	rate reduced	2
<i>A. brachyrhynchus</i>	Iceland/Greenland	× 3.2	mortality rate halved	3
	Svalbard	× 1.7	more reserves	2
<i>A. albifrons</i>	Siberia	× 10	hunting kill increase only × 4	5
	Greenland	× 2	protected 1981	7
<i>A. anser</i>	Iceland	× 4.2	mortality rate halved	3
	Scandinavia	× 4.3	reduced/reserves	2
<i>Branta leucopsis</i>	Svalbard	× 4	protected/reserve	4
	Greenland	× 2.4	protected 1981	6
	Siberia	× 4.3	protected	5
<i>B. bernicla</i>	Siberia	× 8	protected 1971	5
	Svalbard	× 2	protected 1971	2

Iceland. The mortality rate is not significantly correlated with density and may even decrease as numbers increase (Fox *et al.* 1989). Similarly the recruitment rate determines the numbers of most other studied populations in Europe and there is little evidence that density-dependent pressures are coming into play (see e.g. Ebbinge 1990, Fox & Gitay in press). Similarly, in North America the population of the Greater Snow Goose *Anser caerulescens atlanticus* continues to grow following restrictions on its exploitation (Gauvin & Reed 1987).

FUTURE POPULATION LEVELS

What is likely to set the limit on future population growth? Detailed studies on the Svalbard Barnacle Goose may provide clues as to how populations, at least those with small island breeding ranges, such as the populations breeding in the north Atlantic, may be limited. The Svalbard Barnacle Goose population has been studied throughout its range, and its recruitment and mortality accurately assessed (see Owen 1982, 1984, Owen & Black 1989a for details). After a period of exponential growth in the 1970s, following changes in protection on the wintering grounds, the growth rate declined and by the late 1980s numbers seemed to have

stabilized at around 12,000 individuals (Owen & Black 1989a).

Figure 1 shows the mortality rate for the population in relation to total numbers over the 16 years between 1974 and 1989. The mortality rate is calculated from the non-return rates of individually marked birds (10–30% of the population marked; see Owen 1982). The population is fully protected but there is some illegal shooting during the open season in Britain, so the mortality rate in the non-shooting season (March–September), is taken as an index of natural mortality. This includes both migrations (3200 km each way) and the whole of the breeding season. On the breeding area, however, the mortality rate of adults is very low (Owen 1982, Prop *et al.* 1984). The natural mortality rate is very closely correlated with population size for both sexes (Owen & Black 1990a, Fig. 1a). Within the shooting season losses are independent of density, or even inversely correlated (Fig. 1b). Thus the impact of shooting is not keeping pace with population growth, a phenomenon also noted for Pink-footed (Fox *et al.* 1989) and Greater Snow Geese (Gauvin & Reed 1987). For both sexes in Barnacle Geese, the increase in natural mortality causes a significant correlation between mortality overall and density (Fig. 1c).

During the same period, the recruitment rate has declined (Owen & Black 1989a). Thus, as the number of potential

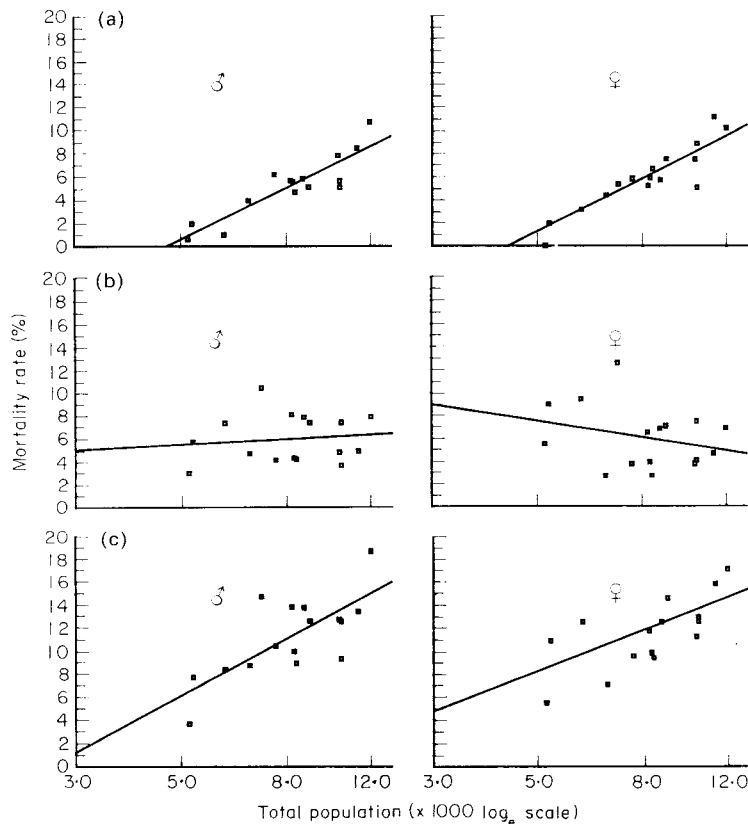


Figure 1. The mortality rates of male (left) and female (right) Barnacle Geese in relation to population size (\log_e scale): (a) for the 7 months of the non-shooting season (March–September); (b) during 5-month shooting season (October–February) and (c) overall. The rate is calculated from arrival in Scotland, i.e. it does not include the losses of young on the first southward migration. Birds of all ages are included, since there is little difference in survival rate of birds of different ages after arrival in Scotland (Owen 1982). Mortality rates are calculated from the non-return rates of individually marked birds (see Owen 1982).

breeders in the population has quadrupled in the last two decades, the absolute number of young produced has not increased (Fig. 2). All the factors acting on recruitment rate are not fully understood but in one year, 1986, losses of production were noted in the proportion of birds failing to nest, nest success, survival to fledging and post-fledging survival (Owen & Black 1991b). The increase in population size has been accommodated largely by increases in density at individual nesting colonies rather than by an expansion of range (Owen and Norderhaug 1977, Prestrud *et al.* 1989).

Acquisition of food during the incubation period is an important prerequisite to nest success; females on a poor food supply have a very high desertion rate (Prop *et al.* 1984). It has also been suggested that competition between broods on the rearing areas leads to the failure of some young to fatten sufficiently to complete the southward migration (Owen 1982, Prop *et al.* 1984, Owen & Black 1989a). Data on the survival rate of juveniles on autumn migration for five seasons were presented by Owen & Black (1989a). In four years survival was high (79–88%) and population size ranged between 7200 and 8400. In 1986, however, when there were 10,400 geese in the population and the number of families was particularly high, survival was only 65%. Data are now available also for 1989, at the peak of population size (12,100 in the previous winter), when survival of young ($n=89$) was only 62%.

Data from more years and an analysis of weather data are needed to establish clearly the relationship between numbers on the breeding grounds, migratory conditions and survival, but evidence of the link, and of the mechanism by which it operates in Barnacle Geese, is accumulating. Similar density-related effects have been demonstrated for a breeding colony of Lesser Snow Geese *Anser caerulescens caerulescens* at La Perouse Bay, Canada. These are manifest through a decline in clutch size (Cooch *et al.* 1989), a reduction of final body size

of young (Cooke 1991), and a lower post-fledging survival rate (F. Cooke pers. comm.).

For the Svalbard Barnacle Goose population, the recruitment rate is negatively correlated with population size (linear regression model, numbers accounted for 30% of the variation in recruitment, $P < 0.025$, one-tailed). Natural mortality is highly positively correlated with population size (Fig. 1, $P < 0.0001$ for both sexes).

Recruitment rate appears to be limited by food supplies on the breeding grounds, complicated by weather on autumn migration. The causes of natural mortality are little understood but these may also be largely brought about by breeding- or migration-related stresses. Females have a higher mortality rate than males and it has been suggested that this is because of the greater energetic demands of breeding which are manifest in losses on autumn migration (Owen & Black 1989a).

The model of Pollard *et al.* (1987) was used to test for density-dependence using the census values (18 years). After 500 simulations, 59 of the simulated values of r_{dx} were less than the calculated values ($P=0.118$). This was confirmed after 5000 simulations ($P=0.113$). This test did not, therefore, establish significant density-dependence at the 5% level. One of the confounding factors is shooting mortality, which is density-independent (Fig. 1). The number of birds shot is declining as the population becomes less accessible to illegal shooting, so that the confounding effect of this 'random' mortality will diminish with time.

LIFE HISTORY STRATEGIES

Geese are characterised by lifelong monogamy and a high degree of female philopatry in the breeding season. Some pairs stay together, despite the fact that they may fail to breed

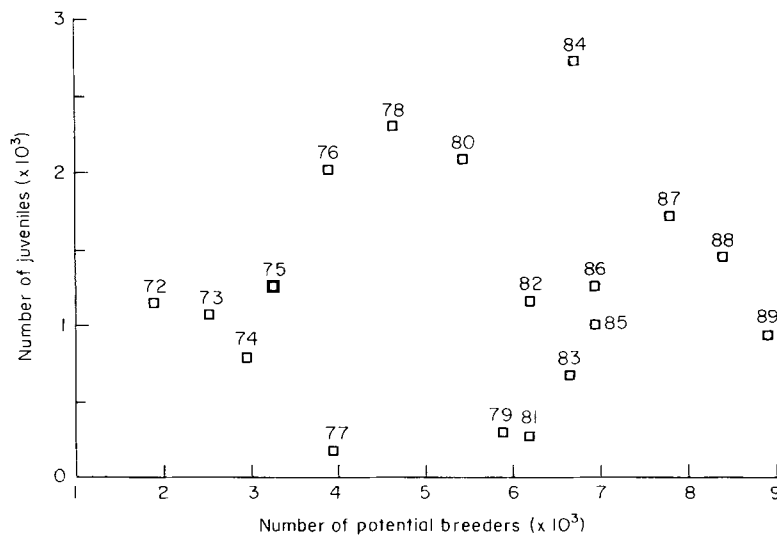


Figure 2. Recruitment of Barnacle Geese (the absolute number of juveniles arriving on the wintering area), in relation to the potential breeding adults in the previous spring (total full-grown geese – total yearlings – 30% of 2-year-olds). Yearlings are calculated as $0.85 \times$ juveniles in the previous year, 2-year-olds as $0.9 \times$ yearlings in the previous year (see Owen 1982). The 30% of 2-year-olds subtracted are the proportion unpaired in their second spring, thus having no chance to breed (Owen 1984). Juveniles are birds of less than 12 months old; yearlings are aged between 12 and 24 months.

successfully, for as many as 14 seasons (Owen and Black 1989b). The cost of re-pairing is a reduced chance of successful breeding in the following year (8%) compared with pairs that remain together (21%; Owen *et al.* 1988).

Female philopatry is very high; 93% ($n=42$) of juvenile female Barnacle Geese return to breed in the area in which they were reared (a small part of the breeding range, usually an island of a few hectares or an archipelago totalling a few hectares, and 95% ($n=222$) of yearling females return to their first-summer moulting site (very probably their rearing site). Established pairs show almost complete fidelity to the breeding site: of 120 pairs studied by Prop *et al.* (1984) at a colony on a 300 × 100m rocky island, over a 5-year period, only 5% changed site and only 6 out of 316 pair/nesting attempts (1.9%) were outside the colony. This is also true of other species; female Snow Geese similarly show a high degree of philopatry (Cooke *et al.* 1975).

Table 2 shows an analysis of pair bond stability during the period between 1973 and 1982 (mean population size 7270; Owen *et al.* 1988) and the same analysis on birds first marked after 1977 and including records for years up to 1988, when the population was much higher (mean size 9605). The rate of separation, whether measured by the proportion of pairs that 'divorced' or by the average theoretical life of a bond (number of stable pair-years divided by the number of splits) is about twice as high during the latter period.

Owen *et al.* (1988) argued that most of the 'divorces' in their study were brought about by accidental separation of mates, usually on migration. They also argued that the chances of separation are greater when the population is larger, because of the greater difficulty of, and time involved in, relocating a separated mate. This may well be true but we suggest that, in time, the behaviour will cease to be adaptive. Figure 2 shows that between the early 1970s and late 1980s, the number of potential breeders in the population has increased three-fold, while the number of young produced has not increased. Thus, on average, the costs of losing a mate, in terms of reduced breeding potential the following year have decreased three-fold. The greater life expectancy (the annual mortality rate has halved since the 1960s; Owen 1982) also increases the chances of future production following a mate change.

Breeding season philopatry has been linked with higher reproductive success in species such as Sparrowhawks *Accipiter nisus* (Newton 1989b) and Goldeneye ducks *Bucephala clangula* (Dow & Fredga 1984). Female geese have much higher energetic demands than males during nesting (Ank-

ney 1977, Ankney & MacInnes 1978) and familiarity with specific feeding areas, to which the female returns year after year, has been shown to be advantageous in increasing the nest success of Barnacle Geese (Prop *et al.* 1984). However, changes in the density of geese using the breeding habitat will affect food availability and perhaps that of nest sites (Owen & Norderhaug 1977). At some stage population growth will affect individual reproductive success sufficiently so that the costs of philopatry will outweigh its benefits (Waser 1988).

The frequency distribution of the number of young reared during the first 14 years of life by females caught as yearlings in two areas of Spitsbergen is shown in Figure 3. Hornsund has a number of large islands suitable for nesting but rather limited tundra rearing areas, whereas Nordenskioldkysten has extensive tundra but few nest sites. During their 12 potential breeding seasons the birds breeding in Hornsund ($n=41$) reared only about half the number of young that the Nordenskioldkysten birds ($n=198$) produced ($P<0.001$, Kolmogorov-Smirnoff two-sample test, one-tailed). The geese were of different cohorts (Hornsund 1972, Nordenskioldkysten 1976), and the chances of breeding during life is influenced by the climatic conditions during the lifespan. However, conditions in the 1970s and 1980s favoured the cohort born earlier (Owen & Black 1989b). It would seem maladaptive for females to stay in an area where their chances of breeding are much lower than in other potential nesting areas. Even if lack of familiarity with a new site meant a loss of breeding potential for one or two years, moving might still have a beneficial effect on lifetime production.

Given a high degree of breeding site philopatry, we would expect that the greater productivity of the Nordenskioldkysten would lead to a higher growth rate in that area as compared to others. This is indeed the case; numbers on the coast increased from just over 1000 to nearly 3200 between 1975 and 1986, an increase of 310%. During the same period the number in the population as a whole (assessed in winter) increased from 6050 to 10,400, an increase of only 74%. The increase on Nordenskioldkysten may have been due in part to immigration as well as to local production but, except for a few years, there is no detailed information on local recruitment. The decrease in numbers of geese on the coast between 1986 and 1989 may indicate that movement to less crowded areas is taking place. A preliminary analysis of movements of marked geese between breeding areas in different years, has confirmed that there was a net emigration of geese from Nordenskioldkysten (Black & Owen unpubl. data).

	1973-1982	1978-1988
% of pairs involved in 'divorce'	3.8	7.9
Pair-years stable/no. of splits	59.0	31.5
Number of pairs in the sample	995	1390
Number of pair-years	2186	3584

Table 2. The pairbond stability of Barnacle Geese during the period 1973-1982, when mean population size was 7270 (from Owen *et al.* 1988) and the same analysis carried out on birds first ringed after 1977 and monitored until 1988 (mean population size 9605). For details of criteria and methods see Owen *et al.* (1988).

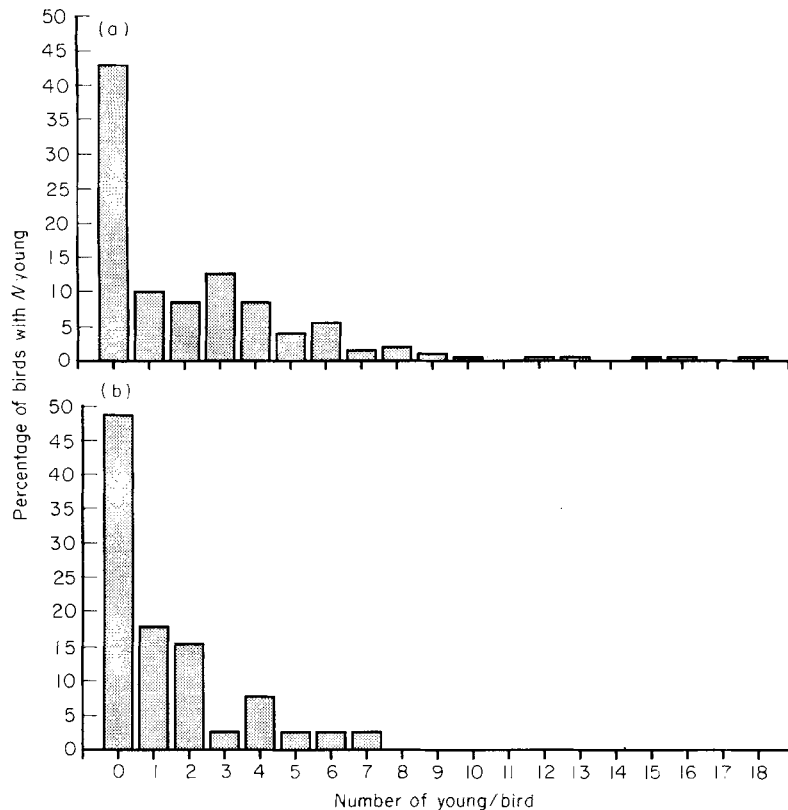


Figure 3. The number of young reared in the first 14 years of life (12 potential breeding seasons) by female Barnacle Geese breeding in two different areas of Svalbard: (a) Nordenskioldkysten, born 1976, $n = 198$; mean no. of young/bird = 2.31 (b) Hornsund, born 1972, $n = 41$; mean no. of young/bird = 1.29. The distributions are significantly different ($P < 0.001$, Kolmogorov-Smirnoff two-sample test, one-tailed) (see Owen & Black 1989b, 1990b).

There are indications, therefore, that the degree of philopatry to the nesting place is decreasing, presumably as prospecting pairs fail to settle on breeding areas which already have a high density of geese. An analysis of site-faithfulness of birds of different ages is needed to establish whether this is indeed the case.

It seems that these two life history strategies may have become less advantageous or even maladaptive for Barnacle Geese now that density-dependent factors are acting on the breeding grounds rather than in winter. Future studies will concentrate on understanding these changes in greater detail and on examining the effect of changes in the population on the lifetime productivity of individual birds.

DISCUSSION

The provision of near-unlimited food on agricultural land and the control of Man's exploitation of the populations has caused increases in many goose populations. Shooting on the wintering grounds is an effective way of controlling numbers but, although such control may be practicable, it may not be politically or publicly acceptable (Owen 1990). In some situations, such as that of the Greater Snow Goose, winter control is probably impracticable because geese become inaccessible to hunters when disturbance is high (Gauvin & Reed 1987, H. Boyd pers. comm.). It seems likely, therefore, that numbers in many populations will continue to increase.

For the Svalbard Barnacle Goose, there is good evidence that there is density-dependent control of recruitment and mortality, acting largely through competition for food on the breeding grounds. The population may well now be near its limit. We suggest that similar controls will act on other populations whose breeding grounds are similarly restricted. This applies to all species breeding in Svalbard, Iceland and Greenland. Too little is known about the Siberian breeders to predict whether and at what stage limitation of their numbers might take place. In North America, Snow Geese have expanded their ranges considerably in Arctic Canada since numbers have increased. Whereas density limitation might operate on individual colonies (Cooch *et al.* 1989), new ones may well become established, as has happened in previous decades.

Implications of further population growth

Goose species have coexisted in some breeding areas without apparent competition; in others, geographical separation, a high degree of philopatry and differences in broad habitat preferences have limited contact between species in the breeding season. This may well not continue, however, if numbers increase further. Madsen & Mortensen (1985) described competition between Barnacle and Pink-footed Geese on moulting grounds in Greenland, and suggested that

the former species would displace the latter should numbers continue to increase.

Pink-footed Geese in Iceland used to be restricted to the highlands; in 1970, a single colony of 10–12,000 pairs represented 75% of the productive population at that time (Kerbes *et al.* 1971). That population has remained stable, whilst other parts of the range, including areas at much lower altitude, have seen considerable growth. The species is now close to, or overlapping with, the range of the Greylag in some areas.

The range of the Barnacle Goose in Svalbard has increased considerably in this century, and it has been suggested that it may be responsible to some extent for the decline of the Brent Goose *Branta bernicla* breeding in Svalbard (Owen & Norderhaug 1977). There is no direct evidence; it seems likely that the Brent decreased for other reasons. However, it seems unlikely that the Brent could recolonize its former strongholds on the west coast, which now has a very high density of breeding Barnacle Geese. The Barnacle is now invading the remaining core breeding area of the Brent in the south-east and is probably able to breed successfully there (Madsen *et al.* 1989).

In North America, expansion of range of the Snow Goose has meant that it has increased in numbers within the range of the Ross' Goose *Anser rossii*. The two species now occur most commonly in mixed flocks and hybrids between them are becoming more frequent (MacLandress 1979, F. Cooke pers. comm.).

Increases in density of birds on the breeding grounds might have consequences for the vegetation of the tundra. Gardarsson (1976) suggested that increase in the density of nesting Pink-footed Geese in Thjorsarver, Iceland, was causing damage to the vegetation and threatening a lasting effect on its productivity. Snow Geese have denuded large areas of vegetation near the densest colonies and these will take many years to recover (Jeffries 1988). Snow Goose colonies move within the vast tundra of north-east Canada but the effects of such changes, should they occur, would be considerable in the more limited tundra areas of the north Atlantic islands.

It seems, therefore, that there are potential dangers to the populations themselves, to related species and to the tundra ecosystem as a whole, should goose numbers continue to increase.

Changes in selection pressures

We have found indications that changes are taking place in the Barnacle Goose that affect the selection pressures for certain life history traits. In the changed competitive situation, both intra- and inter-specifically, it is very likely that the effect of selection pressures on productivity and survival may become modified to such an extent that individual and population characteristics will be affected. For example, Cooke (1991) has demonstrated that increased density in Lesser Snow Geese, has resulted in a decrease in adult size (probably through a phenotypic effect). Such changes may

have implications to the wintering as well as the breeding grounds.

The importance of long-term studies

Predicting future numbers, especially of long-lived species, on short runs of data is imprecise and can give rise to spurious conclusions. For example, the productivity of Greylag and Pink-footed Geese breeding in Iceland declined in the late 1970s. Since numbers were increasing because of an increased survival rate, there appeared to be a density-related decline in fecundity, which led to a predicted stabilisation or even decline in numbers (Ogilvie & Boyd 1976). The decline was due, however, to a run of climatic conditions which acted on both species. A return to a favourable climate resulted in further increases linked to good productivity (Fox *et al.* 1989).

Geese are long-lived and studies of factors affecting individual fitness, using lifetime reproductive success as a measure of productivity, necessarily are long-term. The mean lifespan of male and female Barnacle Geese in the Svalbard population is 10 and 8 years, respectively; of a cohort born in 1972, 10% were still alive in 1986 (Owen & Black 1989b). Changes in life history traits such as those described in this paper are subtle and gradual and can only be detected by long-term studies. Long-term studies of geese are, we argue, essential both for applied and scientific reasons. We need to know the likely future changes in numbers if we are to advise on their conservation or on their damaging effects on agriculture. The changes now taking place in goose populations provide exceptional opportunities to study the way that changes in density affect the individual and the population and the processes by which a population relate to its food resources.

Contributions to the Barnacle Goose study have been made over a long period by a large number of scientists and volunteer observers, whose inputs are gratefully acknowledged. We mention in particular Paul Shimmings, a full-time observer for the Wildfowl and Wetlands Trust, and Rudi Drent and Jouke Prop of the University of Groningen, who provided much data from the Nordenskiöldkysten. The work was supported logistically and financially by a large number of organisations, with major contributions from Earthwatch (USA), The Natural Environment Research Council and Norsk Polarinstitutt.

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