

F. MEHLUM, J.M. BLACK and J. MADSEN

RESEARCH ON ARCTIC GEESE

Proceedings of the Svalbard Goose Symposium,
Oslo, Norway, 23-26 September 1997



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Edited by

F. MEHLUM, J.M. BLACK & J. MADSEN

NORSK POLARINSTITUTT
OSLO 1998

Cover: A pair of barnacle geese *Branta leucopsis* at their breeding site in Svalbard. Photo: F. Mehlum, Norsk Polarinstitut.

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Preface

The current volume consists of 26 peer-reviewed papers on Svalbard geese that were presented at the Svalbard Goose Symposium held in Oslo, Norway, 23–26 September 1997. The Symposium was hosted by the Norwegian Polar Institute and was a follow-up of a similar symposium held in Oslo in 1983. The proceedings of the successful meeting in 1983 were published in a separate volume of *Norsk Polarinstitutt Skrifter*, Nr. 181, in 1984. That volume stimulated new and exciting research initiatives on the barnacle, pink-footed and light-bellied brent goose populations that breed in Svalbard.

The current publication presents many of the highlights from recent years, and it is our hope that this volume will also be of great value both for conservation managers and scientists when identifying priorities in future management and research. A total of 39 participants from six countries attended the symposium, and 30 papers were presented. Not all the papers presented at the symposium were submitted for publication in the proceedings. To broaden the scope of the proceedings, the editorial committee encouraged participants to submit a few additional papers not presented at the symposium.

We are proud to present this collection of papers which encompasses a wide range of topics dealing with the Svalbard breeding goose populations at their breeding sites, at their wintering haunts, and during migration. We would like to thank the authors who contributed to this symposium volume, and we would also like to thank the colleagues who assisted with reviewing the manuscripts. A special thanks to the managing editor of *Norsk Polarinstitutt Skrifter*, Mary Hustad, who did most of the technical editorial work.

Oslo, December 1998

Fridtjof Mehlum Jeff Black Jesper Madsen



Participants of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. (Photo: T.G. Solvang)

Status of the three Svalbard goose populations

JESPER MADSEN, JEFFREY M. BLACK and PREBEN CLAUSEN



Madsen, J., Black, J. M. & Clausen, P. 1998: Status of the three Svalbard goose populations. Pp. 7–17 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.

During the last decades, the Svalbard breeding populations of the pink-footed goose, the barnacle goose and the light-bellied brent goose have been successful in terms of increased population size and the adoption of new staging and wintering areas. They have also successfully adapted new feeding habits in response to the deterioration of traditional habitats, in addition to taking advantage of new opportunities available in the agricultural landscape. The population increases have been brought about by improved survival, more a result of reduced hunting pressures than of improved breeding success. Conflicts with farmers have been exacerbated in wintering and staging areas, but in most situations, local or regional management plans have been implemented to alleviate the potential damage. The populations provide good examples of how management problems and solutions ought to be addressed at the international flyway level.

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Introduction

Three species/subspecies of geese breed in Svalbard: the pink-footed goose *Anser brachyrhynchus*, the barnacle goose *Branta leucopsis* and the light-bellied brent goose *Branta bernicla hrota*. Their population sizes are small compared to other populations of geese in the western Palearctic (Madsen et al. 1996a). Although none of them are critically endangered at present, they all face specific conservation and management problems related to either their breeding, staging or wintering grounds.

During the last 2–3 decades these three populations have been the subject of intensive population monitoring, ringing and studies of population dynamics, ecology, migration and behaviour. This rapid expansion in goose research activity is well reflected in the proceedings from two Svalbard goose symposia (Mehlum & Ogilvie 1984; Mehlum et al. 1998, this volume).

In this paper we give a brief overview of the present status of the three Svalbard goose populations, with special emphasis on the developments since the early 1980s, when the first Svalbard goose symposium was held. We do not describe breeding distribution (see Mehlum 1998, this

volume). A more thorough review of the status is presented by Madsen et al. (1999), Black (1998a, b, this volume), Owen & Black (1999) and Clausen et al. (1999).

Pink-footed goose

Distribution

The pink-footed geese migrate from Svalbard southwards via Norway to autumn staging areas in Denmark and the Netherlands. The wintering grounds include Flanders in Belgium, Friesland in the Netherlands and west Jutland in Denmark. In spring, the population is concentrated in western Denmark before migrating to stopover sites in Trøndelag in central Norway and Vesterålen/Lofoten in northern Norway and from there onwards to the breeding grounds. In severe winters, some geese move to northwestern France (Holgersen 1960; J. Madsen unpubl.). The use of Trøndelag as a stopover area has developed since the late 1980s; it is estimated that in the 1990s almost the entire population stopped over there and subse-

quently in Vesterålen (Madsen *et al.* 1997). Geese have started to use Trøndelag as an autumn stopover as well. Furthermore, during the last decade the autumn staging period in western Jutland has been reduced from 1–2 months to 1–3 weeks, primarily due to food depletion by an increasing number of greylag geese *Anser anser*, which utilise the same areas except for one month prior to the arrival of the pinkfeet (Madsen 1999). Consequently, the arrival of pink-footed geese in Friesland in the Netherlands has advanced.

The Svalbard breeding population is geographically separated from the Iceland/Greenland breeding population which winters in the British Isles (Mitchell *et al.* 1999). On the basis of ring recoveries, it was estimated that in the 1970s there was an exchange between the two populations of a few hundred individuals per year (Ebbinge *et al.* 1984). In the 1990s, intensive neck-banding and resighting have been carried out in both populations. In the Svalbard population, a total of 645 geese have been ringed by the National Environmental Research Institute (NERI), Denmark, during 1990–1995. The average annual exchange of individuals is calculated at 0.7%. At the population level, this represents 246 individuals out of an average total population of 32,000 individuals. The majority of the exchange seems to take place in severe winters (Madsen *et al.* 1999).

Population size and trends

Coordinated population and age counts have been carried out since 1980. Annual population and age counts have been organised since 1991 by NERI together with Dutch collaborators in October/November with synchronised counts in Denmark and the Netherlands. In an attempt to reconstruct the population development in the 20th century, Madsen (1982) used the annual maximum figures recorded in Denmark in spring and autumn. With some reservations these figures are believed to reflect overall population trends. The population seems to have increased in three steps during the twentieth century: (1) from approximately 10,000–12,000 individuals in the 1930s–1950s to 15,000–18,000 in the 1960s–mid 1970s, (2) from 15,000–18,000 to 25,000–30,000 individuals in the 1980s and, (3) from 25,000–30,000 to 32,000–34,000 in

the 1990s, with an unprecedented peak number of 37,000 in the autumn of 1997 (Fig. 1).

Breeding success/survival

The proportion of juveniles recorded in the autumn population since 1980 has varied between 6% and 30% annually without any significant trend, with an average of 16.8% (Fig. 1, Table 1). Average brood size (recorded during 1980–1983 and from 1991 onwards) was 2.03 (Madsen *et al.* in press).

Based on an analysis of ring recoveries, Ebbinge *et al.* (1984) calculated that the annual adult survival rate increased from 0.71 during 1955–1974 to 0.85 during 1975–1983. Based on capture/resightings of neck-banded individuals, Madsen & Noer (1996) estimated annual adult survival rate at 0.84 during 1990–1996. The two methods applied are not directly comparable, but the suggestion is that survival rate has improved during the last four decades.

The pink-footed goose is the only quarry species of the three Svalbard populations, with an open season in Svalbard, mainland Norway and Denmark. Spring shooting was banned in Denmark in 1955 and in Svalbard in 1975. In Belgium, the species has been fully protected since 1981, but most of the pinkfoot wintering area has been protected from hunting already since 1958 (Kuijken & Meire 1987; Meire & Kuijken 1991). In the Netherlands, the species has been protected since 1976 and in Germany since 1977. The annual hunting bag (early 1990s) is estimated at ca. 3000 individuals, with the majority killed in Denmark (Madsen *et al.* 1996b). Thus, shooting is a major contributor to annual mortality. The data suggest that the stepwise increase in population size is most likely related to reduced hunting mortality due to the gradually increasing protection.

A total of 344 pink-footed geese caught and neck-banded in Denmark during the springs of 1990–1992 were X-rayed before release to study the frequency with which shotgun pellets occurred in body tissue (outside the gizzard) and the possible effects on subsequent survival. In first-winter birds, which had experienced one hunting season, 25% of individuals were carrying shotgun pellets, whereas in older birds, 36% were carrying pellets (Noer & Madsen 1996). An analysis of survival of 'carriers' of shotgun pellets versus 'non-carriers' showed that 'carriers' had a signi-

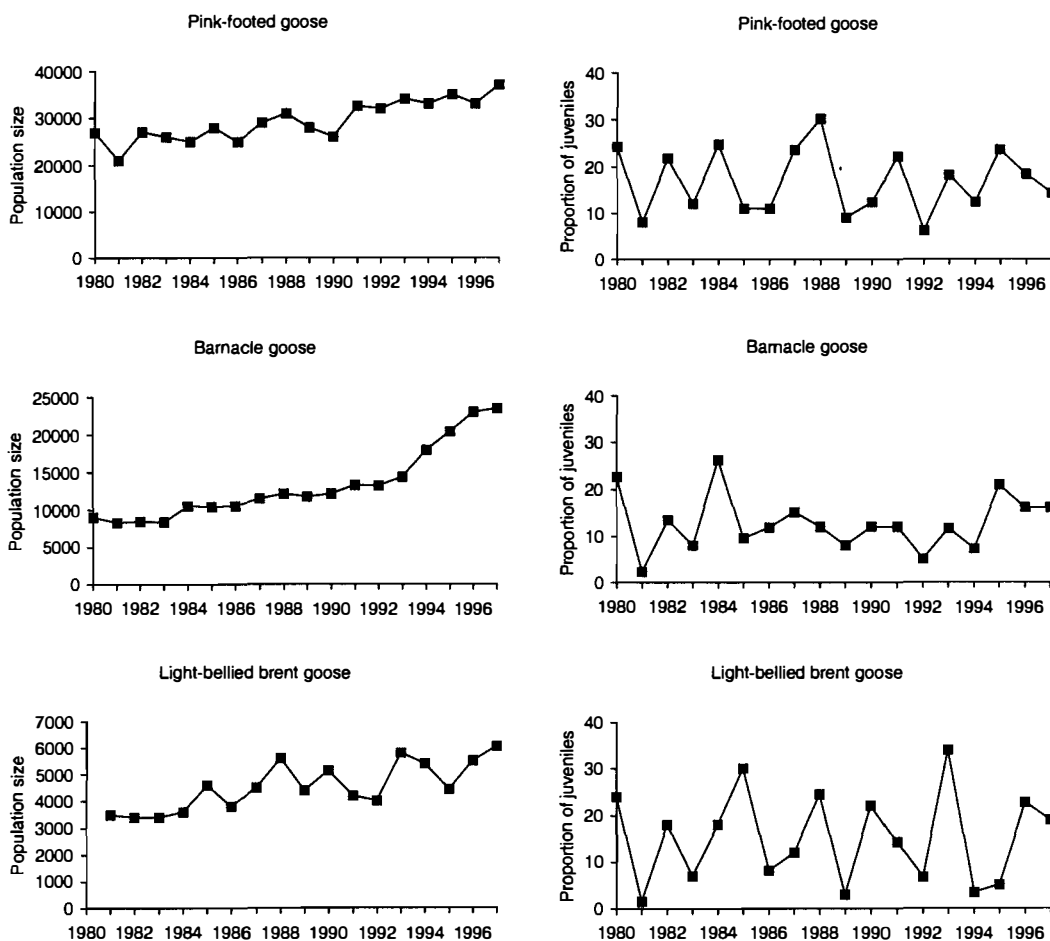


Fig. 1. Trends in population size and annual breeding success of the three Svalbard breeding populations of geese, 1980–1997, as assessed on the wintering grounds. Sources: pink-footed goose and light-bellied brent goose: NERI; barnacle goose: WWT.

ificantly lower survival rate (0.77) than 'non-carriers' (0.87) (Madsen & Noer 1996). At present, however, it is not possible to conclude whether this

is an effect of the pellets (injuries or lead poisoning) or because some individuals in the population for unknown reasons are more exposed to hunting than others.

Table 1. Mean annual breeding success (% juveniles) of the three Svalbard breeding populations of geese, 1980–1997. CV: coefficient of variation. Sources: pink-footed goose and light-bellied brent goose: NERI; barnacle goose: WWT.

	Mean (% juvs.)	CV (%)	Range (% juvs.)
Pink-footed goose	16.8	41.6	6.2–30.2
Barnacle goose	12.8	47.6	2.3–26.2
Light-bellied brent goose	15.2	64.8	1.5–33.9

Conservation and management concerns

Reporting of the high rate of shotgun pellets in body tissues of pinkfeet geese, for which Danish (and Norwegian) hunters are responsible, has given rise to a national Action Plan to improve the situation in Denmark (also for Danish game in general).

Presently, outside Svalbard, pinkfeet geese rely almost entirely on farmland for feeding. This

causes agricultural conflicts throughout the range, except for Belgium where the geese primarily feed on extensive grassland outside the growing season (Madsen *et al.* 1999).

The earlier departure of pinkfeet from Denmark to the Netherlands in autumn has caused an increase in crop damage in the Netherlands. Likewise, earlier departure from Denmark in spring has given rise to increased damage in central Norway, while giving a relief to the problems in Denmark. This is an example of how national management policies and natural phenomena in one country may affect other range states (Madsen & Jepsen 1992).

In Vesterålen in northern Norway, farmers have complained about damage caused by pinkfeet geese to early grass in spring, especially in fields where sheep and lambs are released at the same time as the geese are present in the area. In Trondheimsfjorden, farmers complain about damage to grass and newly sown cereal fields. Due to the authorities' lack of response to these complaints, the farmers in Vesterålen organised a campaign in 1993–1994 (and have continued in some areas since) to scare the geese from the fields. Consequently, the geese staging in these areas stayed for a shorter period than geese in areas where no efforts were being made to scare them off (based on studies of neck-banded individuals). The geese remaining in disturbed areas did not accumulate fat and nutrient stores for subsequent reproduction as well as those in undisturbed areas. Subsequently, geese from disturbed areas did not breed as successfully as geese from undisturbed areas (revealed in the subsequent autumn when they returned to Denmark and the Netherlands) (Madsen 1994, unpubl.).

In Norway, a national management plan to reduce damage conflict caused by geese is now being implemented (Norwegian Directorate for Nature Management 1996; Bø *et al.* 1998, this volume). At the time of writing, a plan for solving the conflicts in Vesterålen is being implemented. There is, however, increasing conflict in central Norway which has still to be addressed.

In spring, pinkfeet in Denmark feed on newly sown cereal and pea seeds. By feeding on these seeds, the geese are exposed to pesticides used as seed dressings. Pea seeds are often treated with Thiram which can easily be ingested by the geese in an amount which could have sub-lethal effects on reproductive parameters (Madsen 1996). The potential poisoning of pinkfeet through intake of

Thiram-treated pea seeds has been addressed. Because of its negative environmental impacts (not only to geese), the use of Thiram has now been banned in Denmark.

Barnacle goose

Distribution

In late August or early September, barnacle geese start their fall migration from Svalbard to the southernmost island, Bjørnøya, some 250 km south of the main group of islands. They stay there for up to three weeks until favourable winds trigger migration south (Butler & Woakes 1998, this volume). Some birds probably migrate directly from Spitsbergen to the wintering grounds on the Solway Firth in northern Britain (Owen & Gullestad 1984).

The wintering range is small, the birds staying within ca. 5 km of the Solway coast and ranging along it to sites no more than 50 km apart. In late April or early May, the birds begin the first stage of their spring migration by moving to Helgeland, an area with a number of archipelagos up to 50 km off the western coast of mainland Norway (Gullestad *et al.* 1984). The second leg of the spring migration is made in the second half of May with the geese staying in the southern part of Spitsbergen before reaching the nesting areas at the end of May.

More than 8000 birds have been individually marked in studies by the Wildfowl & Wetlands Trust (WWT) and this ringing has confirmed earlier findings by Boyd (1961) that the Svalbard population is discrete from the East Greenland and Russian populations, with only 0.1% emigration and no recorded immigration (Owen & Black 1991a).

Population size and trends

The numbers of geese in the population between 1980 and 1997 are shown in Fig. 1. In the mid-1940s there was considerable disturbance on the wintering grounds from wartime activities and heavy shooting; the lowest ever count was in 1948,

when only 300 geese were found on the Solway (Owen & Norderhaug 1977). The geese were protected from shooting in Britain in 1954 and in Svalbard in 1955 and this, with the establishment of the National Nature Reserve (NNR) at Caerlaverock in 1957, led to a recovery in numbers, to 3000–4000 birds in the 1960s. Further increases, to the level of around 14,000 in 1995, followed the establishment of WWTs reserve at Caerlaverock in 1970, and the declaration of breeding sanctuaries on the main island sites in Svalbard in 1973. The population appeared to have experienced six brief phases of stability (ranging from 2–7 years) or steps prior to further expansion (Black 1998a, b).

In the autumn of 1996, a total of 19,200 were counted and a further census in spring 1997 yielded 23,000 birds. These high numbers were confirmed in the autumn of 1997, when 23,500 geese were counted. Few birds carried rings from the Greenland or Russian populations, so it was likely that the birds represented the Svalbard stock. One explanation for the increase could be that the birds have been increasingly lagging behind on migration (there is increasing evidence of this) and that the traditional October count in recent years was carried out before the whole population had arrived on the Solway.

Breeding success/survival

Age counts have been performed annually since 1958 by WWT (see Pettifor et al. 1998, this volume). Breeding success is variable in the population, dependent on the lateness of the spring in Svalbard (Owen & Norderhaug 1977). As the number of birds in the population has increased, breeding success has become generally lower and, in recent years, less variable. During 1958–1969, the average annual proportion of juveniles was 23.7%, during 1972–1982 18.6%, and during 1983–1995 12.4% (Owen & Black in press). This decline is caused by competition for resources in the breeding area. This affects the age of first breeding, brood size, survival to fledging and success of migration. Hatching success varies with the availability of food resources on nesting islands. Food availability also influences the time the female is absent from the nest; the number of young reared on different breeding areas varies with the availability and quality of food resources on the rearing areas (Prop et al. 1984; Owen 1987).

In some years, losses of up to 35% of young can be sustained on autumn migration because some young are unable to lay up sufficient reserves for the journey. This is related to the hatch date of the young, limited food resources in the breeding areas and competition among families for limited food resources (Owen & Black 1989a).

In the 1960s, the population was relatively stable with an annual rate of recruitment and mortality averaging about 25% (Owen & Norderhaug 1977). After 1970, mortality declined again to between 10 and 15%, allowing numbers to increase further (Owen 1982). These changes in population size have been caused by a change in the underlying mortality rate rather than variation in breeding success (Pettifor et al. 1998, this volume; Tombre et al. 1998, this volume). Indeed, in the 1980s and early 1990s, the population continued to increase despite declining productivity. There are indications in recent years that the increases in numbers on the breeding grounds and the implied increased competition for food have affected the mortality rate of adults as well as young during the autumn migration. Whereas mortality from shooting on the Solway has seen a relative decline in recent years, the rate outside the shooting season has increased in both males and females, suggesting higher losses during migration (Owen & Black 1991b). Further analyses are required to determine in detail the changes in mortality rates in recent years and their causes.

Conservation and management concerns

The barnacle goose was given full legal protection from hunting in Svalbard in 1955 and it remains protected there. In 1973, 15 bird sanctuaries were established along the west coast of Spitsbergen, with the aim of protecting the breeding sites of eider ducks *Somateria mollissima* and geese. Access to these sanctuaries is completely prohibited during the nesting season and is by permit only at other times during the summer. In 1982 and 1983 surveys during the nesting period established that no fewer than 70% of nesting barnacle geese were found within these sanctuaries (Prestrud & Børset 1984). Since that time, with the growth of populations in unprotected areas, notably the inland valleys and Nordenskiöldkysten, the pro-

portion nesting on sanctuaries has probably decreased (see Mehlum 1998, this volume).

Islands in the Helgeland archipelago used in spring are also intensively managed for eider down and are jealously guarded by their owners. The eider ducks come ashore to nest at the same time as the barnacle geese are staging, so the farmers ensure that the islands are undisturbed, giving effective protection of feeding areas for the geese. The Directorate for Nature Management have plans to give the area the more formal protection of a designation as a National Park. This would protect not only the habitats but the cultural life on these remote areas and the relationship between the human inhabitants and the wildlife. However, on some of the islands the traditional hay cutting/sheep grazing has been abandoned and the islands become partially overgrown. Increasingly, the barnacle geese have abandoned the small islands and have moved on to improved pastures on the mainland and the larger islands (Black *et al.* 1991; Prop & Black 1998, this volume). Conflicts between farmers and geese have arisen and the Directorate for Nature Management has implemented a management plan to alleviate the problems (Bø *et al.* 1998, this volume).

In Britain, barnacle geese have been protected by law since 1954, though in later years illegal shooting still accounted for some mortality (Owen 1982). The policing of the various areas by conservation agencies and responsible wildfowlers has, however, improved markedly in recent years, and the proportion of the population and probably the absolute number of geese taken illegally has declined to a level which no longer impacts on the overall population.

On the Solway Firth, geese have caused a problem for farmers for many years, and a number of farmers have applied for licences to shoot geese in order to protect their crops. Since 1993–1994, a single farmer has been granted a licence by the Scottish Office to shoot a limited number of geese (in 1995 and 1996, a limit of 12 birds was imposed). WWT took the Scottish Office to judicial review on the grounds that the granting of the licence was unlawful under EU legislation. The matter was settled out of court in WWT's favour in 1996, with the Scottish Office paying the major part of WWT's costs. The conditions under which WWT withdrew its petition for judicial review will probably mean that no licences will be granted in future unless the law or the conditions are changed.

The National Nature Reserve on the Solway Firth was established at Caerlaverock in 1957 with the expressed purpose of protecting the feeding areas of the geese. The Reserve was extended in 1970 when WWT took over the lease of the major part of the reserve and the surrounding farmland (Owen *et al.* 1987). WWT has since extended its holding and now manages more than 400 ha of land at Caerlaverock. In 1994, the Royal Society for the Protection of Birds purchased 200 ha of land at Mersehead, in the Southernness area and some of this is managed as goose pasture and has resulted in the whole area becoming more important.

In 1993 Scottish Natural Heritage established a Goose Management Scheme by which farmers in the main goose areas on the Solway could be paid for tolerating geese on their land and this has done much to alleviate the conflict. Another scheme, the Merse Management Scheme, pays grants to farmers to improve the grazing of the merses in order to improve their value for wildlife, including geese. If numbers do not increase further, these two schemes, when in full operation and refined, should secure the future of the population on the Solway.

In November 1995, conservation agencies in England, Scotland, Norway and Svalbard came together in a seminar to discuss the development of a strategic plan to conserve and manage the population throughout its range. The plan has now been finalised (Black 1998a, b, this volume). The plan is in a format which has been agreed by the parties which will fulfil the obligations of range states under the Agreement on the Conservation of African-Eurasian Migratory Waterbirds which was signed by the U.K. and Norway in 1998. The framework provided by this plan will ensure coordinated international action for the protection of this population and will lead, in all range states, to action being taken to secure the protection of all the habitats and sites on which the population depends at every stage.

Light-bellied brent goose

Distribution

The East-Atlantic light-bellied brent geese migrate

from Svalbard southwards along the western coast of Norway to autumn and wintering staging areas in Denmark and at Lindisfarne in northeast England. The use of Lindisfarne as a regular staging area in autumn and winter by almost half of the population is a new phenomenon that developed during the 1980s (Clausen et al. 1998). In severe winters, most geese move to Lindisfarne, but hundreds of birds also move to the Netherlands (Clausen et al. 1998, Clausen et al. 1999). In spring, the population is concentrated in north-western Denmark before migration to the breeding grounds in Svalbard (Mehlum 1998, this volume; Madsen et al. 1998a, this volume) and Kilen in northern Greenland (Clausen & Bustnes 1998, this volume; Clausen unpubl.).

The recent recognition of the link between the Svalbard and North Greenland breeding light-bellied brent geese represents a change in the traditional view of the North Atlantic flyways of light-bellied brent geese (Clausen & Bustnes 1998, this volume; Clausen et al. in press). Traditionally the North Greenland breeding birds have been linked to the eastern Canadian population which breeds in High Arctic Canada and migrates over Greenland via Iceland to winter in Ireland (Salomonsen 1958).

Population size and trends

Since 1980, coordinated population and age counts have been carried out, by combined efforts of observers in Denmark and Lindisfarne (Madsen 1984; Clausen et al. 1998). The knowledge of the population size prior to the 1950s is only vague. Based on counts of migration along the Norwegian coast in the late 19th century, Salomonsen (1958) suggested that the population may have numbered >50,000 individuals at that time. By 1954–1955, the population had crashed to 4000 birds (Salomonsen 1958). Reasons behind the decline are discussed in detail by Salomonsen (1958) and Madsen (1987). The population continued to decline during the 1950s and 1960s, when Norderhaug (1969) estimated a population of 2750 for the 1965/66 wintering season, and Fog (1972) estimated 1600–2000 birds for the years 1967–1971. Coordinated population counts are not available for the 1970s, but counts from the two spring staging areas at Nisum Fjord and Agerø showed a steady increase in numbers during the 1970s, with

an apparent annual growth rate of 7% (Clausen et al. 1998). Since 1980 a steady but slightly slower population increase has occurred, from 3450–4000 individuals in the early 1980s (Madsen 1984) to 4550–6000 individuals in the mid 1990s. This represents an annual growth rate of 3.4% (1982–1997, Clausen et al. 1998; Clausen unpubl.) (Fig. 1).

Breeding success/survival

The proportion of juveniles recorded in the autumn population since 1980 has varied between 1.5% and 33.9% annually without any significant trend, and with an average of 15.2% (1980–1997). Average brood size on the breeding grounds ranges from 2.36 to 3.44 (data from 1985, 1987, 1989, 1995) and upon arrival to the wintering areas from 2.3 to 3.33 (data from 1988–1991, 1993, 1996–1997) (Clausen et al. 1999; Clausen unpubl.).

Based on the population counts and juvenile proportions, Clausen et al. (1998) calculated an apparent survival rate of 0.87 for the years 1982–1994, and adding data from 1995–1997 does not change the estimate (Clausen unpubl.). In some years, the juvenile segment of the light-bellied brent goose population suffers from high over-winter mortality.

The present survival rate may represent an improved survival compared to the years before 1972, when the light-bellied brent goose was a quarry species in Denmark. Boyd (1959) calculated an annual survival rate of 0.83 by use of recoveries of birds marked on Spitsbergen in 1954 (most birds were reported as shot). Fog (1972) estimated an annual harvest ranging from 150 to 300 individuals, equivalent to 8–18% of the then known population of 1600–2000 individuals; however, that estimate of the harvest rate is conservative (Madsen unpubl.). Assuming the present natural survival rate of 0.87 and additive hunting mortality, the survival rate may have been 0.69–0.79 during the late 1960s.

Conservation and management concerns

Until the mid-1980s, the light-bellied brent goose population regularly used six staging areas and

resorted to natural feeding habitats, i.e. *Zostera* algae beds and saltmarshes (Madsen 1984; Clausen *et al.* 1998; Clausen & Percival 1998, this volume). Since then several changes in the wintering strategy of the population have occurred:

- (1) The population has changed the timing of site use. Birds now arrive from the breeding grounds directly to several sites; earlier all birds moved via the Danish Wadden Sea. Birds also now leave the autumn and winter staging areas earlier in order to utilise Lindisfarne earlier and more regularly than before (Clausen *et al.* 1998);
- (2) The population has begun to use three new sites which during the 1990s have achieved international importance (1% criteria) (Clausen *et al.* 1998 in press);
- (3) The population has changed distribution and habitat use within the six regular sites (Clausen & Percival 1998, this volume);
- (4) Lindisfarne has become a regular wintering site and the Netherlands have developed as ice-winter refuge for a significant proportion of the population (Clausen *et al.* 1998).

Apparently, the changes have been driven by habitat loss (of *Zostera* beds) in combination with increased goose utilisation (due to the general population increase), whereby the remaining *Zostera* stands become depleted earlier than they did prior to the mid 1980s. In addition, habitat degradation in terms of saltmarsh mismanagement has taken place, particularly at the former main spring staging area Nissum Fjord (Clausen & Percival 1998, this volume).

The present wider dispersal of the population may be seen as a positive development despite the fact that part of the change has been driven by habitat loss and degradation. By being spread over more sites, the population is less vulnerable to future incidents of habitat loss in the staging areas.

Conservation and restoration of *Zostera* beds are of high priority in Denmark. Beds have diminished or even disappeared in most estuaries in Denmark due to eutrophication. Large-scale investments in wastewater treatment plants have been made since the mid 1970s, with enforced efforts since 1990, whereby the total national phosphorus discharge to coastal waters has been reduced. The expected improvements in *Zostera* stands have not been evident yet, possibly because simultaneously planned reductions in nitrogen

discharges from agricultural areas have not been met.

Formerly, most geese arrived at Lindisfarne and northwestern Denmark after the peak of hunting. With the changed winter dispersal, brent geese now occur during periods of intensive hunting in all staging areas (except Nissum Fjord). At Lindisfarne the brent geese are now frequently disturbed by hunters in their main feeding areas (Percival & Evans 1997). To what extent the light-bellied brent geese are disturbed by wildfowling activities in Denmark has not been thoroughly quantified, but all sites used by the geese in Denmark will, nevertheless, be given shooting-free reserves, in connection with the establishment of a new national reserve network in all Danish EU Special Bird Protection Areas during 1993–1998 (Madsen *et al.* 1998b). Likewise, a shooting-free reserve in the main feeding area of the brent geese at Lindisfarne was established during autumn 1997 (S. Percival, pers. comm.).

The major conservation problem within the wintering areas is management of the saltmarshes. These could be improved considerably at most sites used by the brent geese (Clausen & Percival 1998, this volume). Brent geese have recently begun to use agricultural areas at Lindisfarne, around Randers Fjord and Agerø, which may lead to future agricultural conflicts (Percival & Anderson 1998, this volume; Clausen *et al.* 1999). Management of saltmarshes and procedures to avoid agricultural conflict in the future are thus the main objectives of an international flyway management plan.

Discussion

All three Svalbard breeding populations of geese have increased in numbers during the recent 3–4 decades. The earliest increases were most likely due to improved survival as a result of the closure to hunting (or reductions in hunting pressure) and egg harvesting. It is too early to interpret the reasons behind the recent upsurges in numbers. None of the populations has experienced an observable increase in overall breeding success, suggesting that improved survival is the principal mechanism (e.g. Pettifor *et al.* 1998, this volume; Tombre *et al.* 1998, this volume).

When we compared the breeding success of the

three populations, there was not much difference in the mean annual proportion of juveniles in the wintering flocks (Table 1). Light-bellied brent geese showed a higher degree of variability in breeding output compared to pink-footed goose and barnacle goose. In years with poorest breeding success, pink-footed geese were not as seriously affected as the other two species.

There is a strong positive correlation in the annual breeding success between pink-footed geese and barnacle geese ($r = 0.721$; $n = 18$; $P < 0.001$). There was a positive but not significant relationship between pink-footed geese and light-bellied brent geese ($r = 0.410$; $P > 0.05$), and likewise between barnacle geese and light-bellied brent geese ($r = 0.366$; $P > 0.05$). Pink-footed geese and barnacle geese both breed in Spitsbergen, and it is likely that their breeding success is governed by the same climatic conditions. The majority of the light-bellied brent geese breed in Tusenøyane south of Edgeøya. As shown by Madsen et al. (1998a, this volume), their breeding success is to a high degree affected by pack-ice conditions which are a proximate indicator of predation pressure by polar bears *Ursus maritimus*. Ice conditions in southeast Svalbard may not necessarily reflect the overall climatic conditions in the Svalbard area and, hence, fluctuations in breeding success of light-bellied brent are partly out of phase with the other two species. Furthermore, a segment of the light-bellied brent goose population breeds in northeast Greenland (Clausen & Bustnes 1998, this volume), and its contribution to the overall breeding success is still poorly understood.

All three populations face various conservation management problems outside the breeding grounds. The pink-footed goose faces the most complex management problems, providing a good example of a population requiring international collaboration regarding hunting management issues (hunting kill rates, crippling) and agricultural crop damage conflicts (both in autumn and spring). For all three populations, increasing crop damage conflicts can be anticipated in future years, partly because of the increasing population sizes and partly because of the general tendency of increasing use of improved pastures and agricultural habitats. Management problems have been tackled locally or nationally, but without a 'policy analysis' of the ecological requirements and conservation needs of the populations in a flyway perspective. The flyway conservation plan for the

barnacle goose hopefully provides a model for a functioning international collaboration which can eventually be applied to the other two populations.

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Action Plan for goose management in Norway

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Bø, T., Ekker, M. & Lindgaard, A. 1998: Action Plan for goose management in Norway. Pp. 19–28 in Mehlum, F., Black, J. M. & Madsen, J. (eds.): Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skrifter* 200.

In 1996, the Directorate for Nature Management published an action plan for goose management in Norway. The Action Plan covers all the seven Norwegian goose species, which differ significantly with respect to population status and conflict potential. The conflicts between geese and agriculture (farmers) are focused upon and the plan aims to create a common understanding of the need for reducing conflicts and to ensure viable geese populations. As most goose populations spend time in several European countries throughout the year, international collaboration is necessary to achieve the goals outlined in the plan. This paper focuses on the Svalbard goose populations and outlines the main objectives for management of these populations.

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Introduction

During the last few decades, most goose populations throughout Europe have increased in numbers. However, some populations have decreased and may become extinct if this negative trend is allowed to continue. The populations that are growing in numbers are simultaneously expanding their ranges.

There have been significant shifts in habitat use which are related to these expansions, especially with regard to a growing dependence on agricultural land throughout the range of these populations. The situation in Norway is similar to that of other countries with resident or migrant goose populations. During the 1980s a conflict grew between migrant geese and rural agricultural interests, primarily in the form of damage to grasslands and to some extent pastures and cereal crops.

In 1994 the Norwegian Directorate for Nature Management (DN) invited representatives from various organisations to form a working group to draw up an action plan for goose management in Norway. Represented in the working group were two associations representing farmers, the Norwegian Ornithological Society, the Norwegian Association of Hunters and Anglers, the Ministry of Agriculture, the Norwegian Institute of Nature Research, the Governor of Svalbard, and DN. The group's mandate was to address important aspects of

goose management, with particular focus on reducing conflicts between geese and other interests.

The Action Plan discusses the distribution and status of these goose species throughout their range and within Norway. It includes information on population size, trend and distribution, as well as habitat choice, breeding biology and migration routes.

The Action Plan aims to establish goals for future goose population management in Norway and to represent a national action plan for all goose species in Norway, as required by the Waterfowl Agreement under the Convention of Migratory Species. The plan also represents an updated 'handbook' in goose problems. The handbook is published in Norwegian with an extended English summary as DN-report 1996-2.

This paper presents relevant parts from the Action Plan, including the main objectives, general recommendations on selected subjects, research and monitoring needs, and the single-species actions for the Svalbard goose populations.

Background

All goose species, with the exception of the introduced Canada goose, must be managed in accordance with international agreements and conventions. Norway must co-operate with several

Table 1. Summary of the biology and ecology of goose species/populations that normally occur in Norway.

Subjects	Bean goose ¹	Pink footed goose	Lesser white-fronted goose	Greylag goose	Canada goose	Barnacle goose	Brent goose
Population estimates, total population in Europe (individuals)	80,000 (fabalis)	214,000	ca. 20,000	over 200,000	uncertain	220,000	uncertain
Population estimates (Autumn–Winter) Norway	300,000 (rossicus)	33,000 (Spring)	200 (30–50 pairs)	60,000	> 15,000	13,500	5,800
Population trends, last 15 years	unknown	positive	negative	positive	positive	positive	uncertain
Population trends, last 3 years	uncertain/negative	stable	uncertain	slightly positive	positive	stable	positive
Clutch size	uncertain/positive	3–5	4–6	5–6	5–6	3–5	4
Time in mainland Norway	April–Sept/Oct	May + Sept/Oct	May–Aug/Sept	March/Apr–Sept/Oct	all year	April/May + Sept/Oct	May + Sept/Oct
Actual hunting season	10.08–31.01	10.08–31.01	No	10.08–31.01	10.08–31.01	No	No
Hunting season:	21.08–31.10	10.09–31.10	No	(15) 21.08–31.10	21.08–31.10	No	No
Norway (1992–97 period)	–	21.08–31.10	–	–	–	No	No
Svalbard	S, DK, NL/DK, GB	GB, DK, NL	uncertain	ES, NL	N, S	GB	GB, DK
Wintering areas	N, NL, DK, S, GB	N, DK, NL, B	N, FIN, S, RUS, D, H, GR, and others	N, DK, NL, ES	N, (DK), S	N, GB	N, DK, GB
Nations with responsibility for Norwegian populations ²							
IUCN categories	–	–	Vulnerable	–	–	–	–
The Bonn Convention (CMS)	Appendix II	Appendix II	Appendix II	Appendix II	Appendix II	Appendix II	Appendix II
CMS – AEW A (acc. to column)	B	B	A	C	–	A	A
The Bern Convention	Appendix II	Appendix II	Appendix II	Appendix II	Appendix II	Appendix II	Appendix II
EEC – Bird Directive		Appendix II	Appendix II			Appendix I	Appendix II

¹ The Bean goose appears in two distinct breeding populations and differs in some subjects: the Finnmark population to the left/middle-Norway population to the right.² Nation abbreviations: B – Belgium; D – Germany; DK – Denmark; ES – Spain; GB – Great Britain; N – Norway; NL – Netherlands; RUS – Russia; S – Sweden; FIN – Finland; H – Hungary; GR – Greece.

European countries in establishing management goals, methods and regimes on a flyway level. A national action plan for the conservation of biodiversity is presently under consideration. Norway's international obligations are also closely connected to the Svalbard Treaty relative to geese breeding in arctic areas. Pertinent data for the goose species considered in this plan are listed in Table 1.

The most important factors of current concern relate to damage problems, including conflicts with agricultural interests. Other management-related issues are addressed which are related to interspecific competition, overgrazing, introductions of alien species, conservation of protected areas, goose impact on other conservation interests (i.e. protection of rare plants), tourism, disturbance, pollution, habitat destruction and the effects of hunting. The biological and ecological characteristics of each goose species are presented in the context of how these influence the extent and timing of crop damage. Hunting statistics, hunting pressure, options for changing hunting practices, organisation and availability of hunting areas are discussed.

Increasing international interest in managing goose populations across national borders requires common knowledge on goose biology/ecology and understanding of management options, biology and ecology among countries within the range of each species and the flyways of the populations. Our general knowledge of these factors is good. Basic biological and ecological research, when combined with monitoring programs, will aid in filling in current gaps in our knowledge. A strategy that conveys current knowledge to authorities, farmers, and the general public is required.

Main objectives

The future management of geese in Norway should be based on a set of general principles which are in accordance with international recommendations and agreements and effected on a national, regional and local basis. The principles are based on the following main management objectives:

1. Geese represent a biological resource that shall be managed to ensure the continuing

existence of viable populations and their habitats in both the short- and long-term future.

2. Sustainable harvest of huntable populations must be given a proper framework which will allow hunting to function as an effective management tool and simultaneously provide an attractive recreational opportunity.

3. Conflicts between geese and agriculture must be addressed and solved in a way that benefits both geese and farmers.

First main objective includes:

- Carrying out of international obligations.
- Playing an active role in development of international agreements.
- Ensuring that management of the goose populations is based on factual knowledge achieved through monitoring and research.
- Ensuring that local and national management practice is related to agreed upon international strategies and management.
- Hindering/eliminating the escaping of alien species and other influences from introduced species from becoming a threat to wild goose populations, and avoiding a population trend that represents a threat to flora and fauna.
- Authorities, organisations and individuals must take responsibility for the management of the goose populations' habitats.

Second main objective includes:

- The wildlife authorities must establish a framework that ensures necessary flexibility related to changes in size and trend of the populations.
- Ordinary hunting must continue to be a central means to moderate population growth and therefore the potential for crop damage for the huntable species.
- Damage caused by greylag and Canada geese must be prevented through local regulation of populations.
- Killing of geese that cause damage outside the ordinary hunting season must be set to a limit.
- Methods of gathering statistics on harvest yield and hunting effort must be improved and extended to include Svalbard.
- Landowners and their organisations must make arrangements for increasing the opportunity for goose hunting so that hunting can function as a

means of reducing the damage caused by greylag and Canada geese

- Hunters and their organisations must organise goose hunting efficiently so that this method of exploitation is of high quality, humane and ethically justifiable. The frequency of injured geese during hunting must be reduced.

Third main objective includes:

- *All sectors* have a responsibility to maintain viable populations of geese as part of the biodiversity. Consequently the costs associated with the efforts to ensure vital populations and to prevent/reduce crop damage must reasonably be shared among the affected parties.
- Geese management must utilise positive means to moderate conflicts between geese and agricultural interests to the greatest possible extent.
- Increased knowledge of the grazing and damage situation in the most important habitats must be obtained, and methods must be developed to measure the effects of preventive efforts.
- Authorities must contribute economically and administratively so that local management plans can be realised and conflicts reduced to acceptable levels.
- Conflict reduction in areas with crop damage requires a systematic discussion in co-operation with the affected parties of population considerations on the range of problems and possible preventative measures.
- Goose management and area management must be seen together and be anchored in local management plans to the greatest extent possible.
- Local management plans must establish solutions which are satisfactory for the farmers affected by the conflict, as well as give consideration to geese as a resource for recreation and harvesting.
- Local management plans must reflect the necessary flexibility that corresponds to the dynamic lifestyle of geese with respect to local movements, variation among populations, and response to preventative measures.
- Regular and thorough evaluations of local management plans are important for finding permanent solutions in areas with conflict, and for being to effect a prompt management response in new areas. As a part of the follow-up to local management plans, farmers must be

informed/educated in relation to geese-agriculture problems so that damages are minimised.

General recommendations

Administrative and economic priorities are based on the fact that populations with a negative population trend (lesser white-fronted, bean and brent geese) differ greatly from increasing populations of other species with regard to management options as well as needs. A difference also exists between populations that are hunted (anywhere within their range) and those that are presently not huntable. The third important difference separates populations that are associated with conflict or potential conflict from those that are not.

International obligations and management plans

The working group proposes that the action plan should be considered as a national plan for future goose management in Norway, and as such it complies with the requirements in the Waterfowl Agreement (CMS). International management/action plans for single species must be designed and implemented for the following (in order of priority): the lesser white-fronted goose, barnacle goose, pink-footed goose, brent goose, bean goose and greylag goose. The plans should be finalised for lesser white-fronted, barnacle and pink-footed geese before year 2000. For brent and bean geese, there is insufficient data to finalise single species plans. The working group recommends that the Action Plan be used as a basic guideline to develop regional and local management plans to alleviate the conflict with agricultural interests. A general description of the process of making local management plans is illustrated in Fig. 1.

Local management plans are considered to be essential for reducing conflicts and should be developed in areas with significant crop depredation. Such plans should include cost assessment for various management solutions. It is impossible to determine financial resources needed to implement the recommendations in full before such local management plans are developed. It is clear, however, that these recommendations will lead to a significant change in administrative efforts by

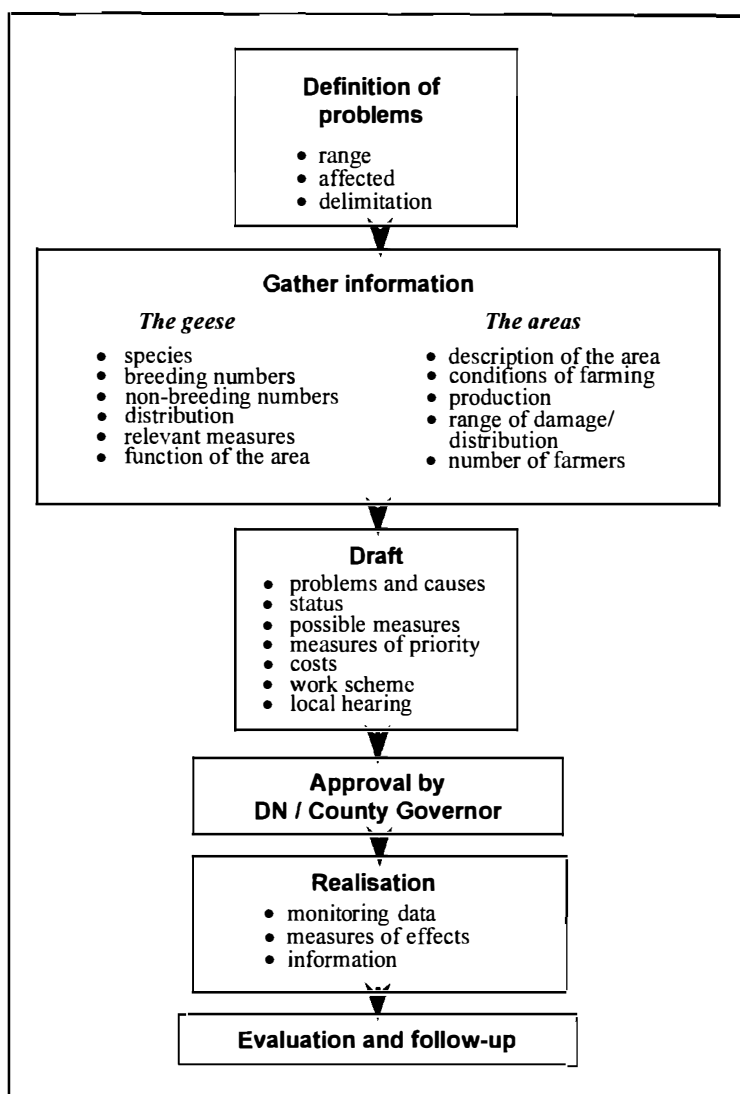


Fig. 1. The process of designing regional/local management plans.

both the governmental agencies and the involved interest groups, thereby increasing the need for funds.

Compensation and damage prevention

Compensation schemes for reducing economic loss to farmers are discussed, as well as examples of such schemes from other European countries. The working group believes that ordinary compensation based on damage assessment and

subsequent payment to farmers may be both unfair and inefficient. Instead, the working group recommends a compensation scheme whereby state funds (from both the Ministries of the Environment and Agriculture) are allocated only to landowners that, in co-operation with local government, have implemented area management practices beneficial to geese. Farmers who aim to prevent damage through scaring or other aversive measures should have access to technical equipment partly financed and provided by the State. The major goose-agriculture conflict areas in

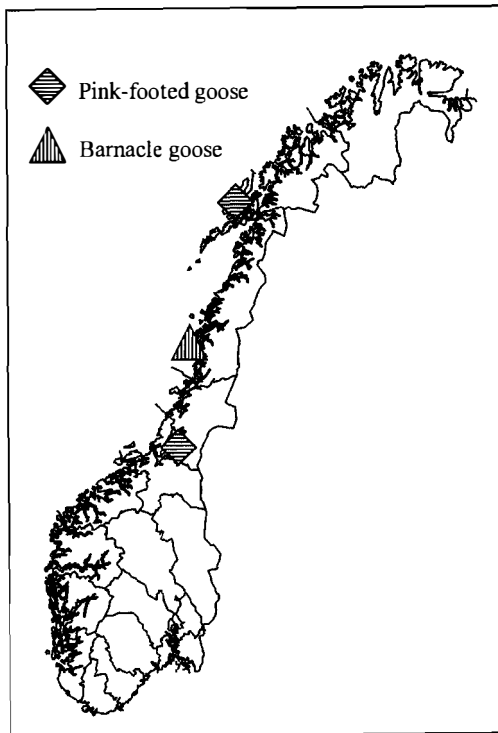


Fig. 2. Main spring staging areas for pink-footed and barnacle geese in Norway. These areas are also the major conflict areas with these species and agriculture.

Norway for pink-footed geese and barnacle geese during the spring migration period are presented in Fig. 2.

Damage prevention methods are listed in the action plan. In general, crop and land-use management practices that divert geese away from damage-prone areas are the preferred strategies for protecting vulnerable crops. In this regard, information and education in preventative techniques are primarily tasks for the farmers' organisations.

Hunting and control

In Norway, hunting is an established practice for meeting management goals relative to reducing crop depredation and/or population size. Different options for the regulation of hunting practices are discussed, and proposals for changing existing regulations are offered. Legislation for species and area management provides a basic framework.

Both are needed to combine population management and land-use planning as instruments to reduce conflict levels. Both governmental and interest organisations should prioritise education and information measures that target landowners and the general public regarding these matters.

Research and monitoring priorities

Research

A considerable amount of research has been conducted on geese internationally. For several species it is natural that research be initialised and chaired by foreign institutions, according to international accepted objectives and priorities. Norway still has some specific research needs and a specific responsibility for monitoring. These activities are not actually research, but rather the use of existing and known methodology to establish the best possible basis for management.

The action plan will not attempt to control the activity of the different research institutions. The plan will give recommendations for the research that is financed through the wildlife authorities. As economic funds for conducting all the desired research tasks are not available, the plan gives priority to research tasks deemed necessary:

1. Map breeding, moulting and migration staging sites for the lesser white-fronted goose. This is considered as necessary follow-up of the Action Plan for lesser white-fronted goose. The mapping is also essential according to the goal of conserving the species as part of the Norwegian fauna;
2. Determine factors that negatively effect the brent goose on the breeding areas in Svalbard;
3. Continue existing research and stimulation to further research on barnacle goose and pink-footed goose, according to plans from the Wildfowl and Wetlands Trust and the National Environmental Research Institute in Denmark.
4. Examine breeding sites and time of breeding for Norwegian greylag geese from central moulting areas, and clarify the effects of hunting on different age groups and of different hunting regimes.

Monitoring

Monitoring in Norway is solely a Norwegian responsibility. The Action Plan suggests the following monitoring priorities:

1. All known staging, breeding and moulting areas for the lesser white-fronted goose, to determine status, population size and trend;
2. The breeding, moulting and possible staging areas for the brent goose, to determine variation and trend in the breeding population;
3. Moulting bean goose in Trøndelag;
4. The neck-banded pink-footed geese in Norway to determine the use of, and changes in, the staging sites;
5. Distribution of barnacle geese in the sites related to area management measures;
6. Breeding population of greylag goose in selected areas, and surveying the effects of different efforts regarding hunting and egg collection if it is permitted;
7. Neck-banded greylag geese in selected localities to evaluate establishment, production, distribution between breeders and non-breeders, and hunting;
8. Effects of preventative measures;
9. Type and extent of damage/economical consequences for the farmer.

Single-species recommendations

The action plan lists the management goals, use of means and delegation of responsibility according to species. For some species, the need for new knowledge can come into conflict with the need for reduced disturbance. Such cases must be closely evaluated before actions are carried out. Below, only species breeding in Svalbard are presented.

Pink-footed goose

The situation of the pink-footed goose population is secure. There are no indications that a change of the population status will occur within a short time perspective. An eventual population increase is expected. Through various research projects and monitoring, the knowledge of what factors effect

the population has recently been improved considerably.

Main objectives

- The population of pink-footed goose shall be maintained at the present level for the time being, until a common discussion has been conducted with authorities in Denmark and the Netherlands.
- The staging sites shall be secured through an extensive co-operation with landowners.
- Sites should be protected through the Nature Conservation Act to secure areas of specific concern for the population.
- It is expected that Danish and Dutch authorities will initialise a flyway plan for the species within a few years. Until such a plan is completed, the Norwegian efforts should be focused on reducing damage and monitoring trends at the staging sites.
- No measures will be carried out in Svalbard, and no further short-term changes in hunting seasons will be made.

Partial objectives

- Farmers shall not alone bear the cost of damage caused by pink-footed goose at the spring staging sites.
- Changes and redistribution at the spring staging sites shall be surveyed. The staging sites in autumn should be examined more closely, particularly to be able to carry out measures to ensure control with the harvest.
- The moulting sites of the pink-footed goose in Svalbard shall be mapped.
- The pre-breeding spring staging sites of the pink-footed goose in Svalbard shall be mapped.

Means

- The use of areas inside the damage-affected areas by geese will be surveyed during 1996.
- Alternative feeding areas for geese in the damage-affected areas shall be bought, cultivated, managed or established through special agreements with affected land users.
- Information material on actual damage preventive efforts will be produced.

- Standard agreements on the division of costs for land users who do not scare off geese will be developed.
- A sufficient proportion of ringed geese in the population will be maintained so that research and monitoring can continue. The effects of the measures that have been carried out so far will be documented.
- Regulation of day and night hunting on the mainland will be introduced in the same way as has been suggested for greylag goose.

Responsible parties

- The County Governor is responsible for surveying the areas that the geese use for feeding and relevant areas of special importance in relation to the staging sites. It is further the County Governors' responsibility to ensure a sufficient follow-up of ringed birds at the staging sites.
- DN is to maintain the necessary contact with Danish and Dutch authorities regarding management and need for co-ordinated efforts, including work on a flyway plan. DN is to make a proposal for regulation of day and night hunting in the next hearing of the Hunting season regulations.
- The Agricultural Organisations are to prepare information material on preventing efforts in co-operation with DN, and make its availability known.
- Funding for efforts that promote reduction of damage, including cultivating/management of an area shall be a priority of both agricultural and wildlife authorities.

Barnacle goose

In an international perspective, the barnacle goose is an example of a successful protection effort. The Svalbard population receives special interest because it is probably one of the best-studied bird populations of the world. The population's importance as a reference population and as a research object is therefore considerable.

Main objectives

- The size of the barnacle goose population shall

be maintained at least at the present level for the time being.

- The staging areas shall be maintained through extensive co-operation with land owners/tenants.
- Area protection by the Nature Conservation Act should be effected to secure areas of special concern for the population.
- The breeding sites in Svalbard shall be protected against disturbance, with the reservation that the relations to the brent goose must be clarified.
- Potential population control should be carried out in the wintering areas or in Svalbard, and *not* on the staging areas.
- An international flyway plan shall be completed during 1996.

Partial objectives

- Affected farmers shall not alone bear costs of damages caused by barnacle geese on the staging areas.
- Foraging areas of traditional importance outside damaged areas shall be conserved or cultivated to maintain sufficient quality.
- The function and value of the population as an object of reference and research shall be given continued priority.
- The technical and financial share of contribution from British and Norwegian authorities and relevant research bodies/institutions will be clarified during 1997.
- The use of habitat in Svalbard by the geese before they establish on the breeding areas must be determined.
- The moulting areas in Svalbard must be mapped relative to possible effects of disturbance.
- The local population in the Oslo area originated from released/escaped birds and shall not be maintained.
- The degree of possible confusion with Canada goose in the hunting season during autumn migration must be determined.

Means

- The area use of the geese within the areas exposed to damage shall be surveyed during 1995 and 1996.
- Alternative feeding areas for geese in the areas exposed to damage is to be bought, cultivated,

managed or established by special agreements with affected farmers.

- Information material on relevant damage preventing measures will be produced. Standard agreements on division of costs for farmers who do not scare off geese will be made.
- A sufficient amount of ringed geese in the population will be maintained so that research and monitoring may continue and the effects of attempted measures can be determined.
- A regular routine of monitoring on the breeding areas will be established.

Responsible parties

- DN shall initiate and fund a joint flyway plan in co-operation with Scottish Natural Heritage according to international standards given in the Waterfowl Agreement. This plan shall be a model for later similar plans for other species. This work must be completed during 1996. Consideration for affected farmers on the staging areas must be an integrated part of the plan.
- The farmers' organisations will together with DN produce information material on relevant preventative measures and ensure that these are publicised.
- Subsidies for measures that promote damage reduction, including cultivating/managing of areas, will be given priority from both agricultural and wildlife authorities.
- Cultivation of formerly used areas will be considered by regional authorities to ensure that environmental qualities are maintained and that consideration for feeding geese is balanced against other interests of environmental protection.
- The Governor of Svalbard and the Norwegian Polar Institute are responsible for establishing routines for monitoring and mapping moulting areas and areas used before breeding.

Brent goose

The Svalbard brent goose population has not had the same growth in population size as most of the other goose species. The reason for this has not been clarified, but it is probable that the quality of the population's breeding areas is not good enough. This could be caused by several reasons,

such as high predation pressure and possible competition with barnacle goose. Because of the low population number, the brent goose must be given special attention. Unlike the other goose species, we lack important information on factors affecting the population.

Main objectives

- The brent goose population shall be maintained at the present level at least for the time being.
- Measures must be undertaken to provide a basis for reviewing the status of the species by the year of 2000.
- The brent goose shall be managed as a particularly vulnerable and demanding species, for the continued survival of the species in Norway, with demands on special attention and particular measures taken at the individual and habitat level.
- Norway should play an active roll in initiating an international flyway/action plan for the brent goose.
- It is important to conserve both existing and former staging, breeding and moulting sites for the geese.
- The range of the population must be mapped.
- The long-term objective should be to increase the population size considerably to ensure continued survival.
- The breeding sites in Svalbard must be sheltered against disturbance and negative influence in all possible ways. This will not prevent conducting measures necessary to gain updated information on migration, production and wintering sites.
- When improved basic data are obtained, an action plan for brent goose, according to the Waterfowl Agreement, must be prepared.

Partial objectives

- Regular monitoring of the size and variation in the breeding population in Svalbard must be established.
- Routines for surveying the annual variation in production of goslings must be established.
- The most important threats to breeding, moulting and wintering sites must be clarified.
- A better knowledge of migration routes and staging sites must be obtained.

Means

- Surveys of the population size and trend in Norway can best be made through routine counting on breeding/moulting sites. These must be conducted with methods that cause the least possible disturbance. Counts on wintering areas must be continued to clarify which part of the population breeds in Svalbard.
- Mapping of migration and staging sites, and determining annual production, can only be achieved through co-ordinated ringing programs and use of satellite telemetry.

Responsible parties

- The Governor of Svalbard will work out a plan for monitoring breeding areas in Svalbard in co-operation with the Norwegian Polar Institute before the 1997 breeding season.
- DN will take the initiative to clarify the status of the ringing data for the species and coordinate such efforts concerning the wintering areas.
- DN and the Governor of Svalbard will take the initiative to clarify whether there is real competition between brent geese and barnacle geese on the breeding grounds in Svalbard.
- DN will take the initiative to begin work on an international action plan for the Svalbard population of brent goose.

Epilogue

Since the Action Plan was published in 1996, several actions have been taken. For the Svalbard species, following important topics have been given priority:

- Satellite-tracking of brent geese during spring migration up to the breeding grounds in Svalbard and Greenland.
- Work on the Flyway Plan for the Svalbard barnacle goose population (to be completed in 1998).
- Study of spring migration and change in staging strategy of the pink-footed goose.
- Local management plan for barnacle geese on their spring staging sites in Herøy, Nordland County, has been completed.
- Processes with local and regional management plans for the spring staging sites of the pink-footed geese in Sortland, Nordland County, and in Innherred, Nord-Trøndelag County have been started.
- Monitoring programmes in Svalbard are under development.
- Day and night hunting regulations for the pink-footed goose on the Norwegian mainland was introduced in 1997.
- Survey of extended use of areas of the barnacle geese on spring staging areas in Nordland.

Flyway Plan for the Svalbard population of barnacle geese: A summary

JEFFREY M. BLACK



Black, J.M. 1998: Flyway Plan for the Svalbard population of barnacle geese: A summary. Pp. 29–40 in Mehlum, F., Black, J.M. & Madsen, J. (eds.): Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skriftr 200*.

This paper summarises the recently completed 'Conservation and management plan for the Svalbard population of barnacle geese.' published by the Directorate for Nature Management and the Scottish Natural Heritage (Black 1998). The aim of the Flyway Plan is to consolidate current information about the Svalbard population of the barnacle goose *Branta leucopsis* (including its biology, behaviour, ecology, population status and dynamics, international interests and conservation issues) and thereby establishing a unified understanding and reference document for a bi-lateral, international agreement concerning the future conservation and management of the population and its habitats. The paper outlines the main sections of the flyway conservation and management document, including rationale, history and current status of the population, current protection, policies and management, research needs and future studies, specified limits, long-term or ideal management objectives, and the action plan: an outline for the future.

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Introduction: rationale for the Flyway Plan

The Svalbard barnacle goose population is one of the most celebrated wildlife management and conservation success stories in the United Kingdom and Norway. It was through proactive wildlife policy and the establishment of well-managed refuges that the population recovered from critically low numbers (Owen & Norderhaug 1977). Due to the sustained increase in numbers, a proportion of the population has overflowed what is believed to have been the historical range. Where this expansion is near rural communities, as on the wintering grounds and spring staging areas, the geese are often not welcome on agricultural land. Therefore, the population currently endures the unlikely status of being 'threatened' and considered a pest in some situations.

The Flyway Plan for the Svalbard barnacle goose population is useful because of the increasing need for cooperation and conciliation among countries that the goose visits. The outcome of management at one end of the range can affect,

and has affected, numbers and distribution at the other end of the range (Owen & Norderhaug 1977; Owen et al. 1987).

Thus, before the population and its habitats can be managed, it is necessary to establish a basic and common description of the population's history. Today's actions, or lack of action, will determine the future of the population and its habitats.

The problems and concerns that managers face, specifically with regard to reserve management and the adjacent farming communities, are similar throughout this bird's range. The research that is needed to better understand past events and predict future trends requires the continuation of collaborative efforts. Pursuing a set of research priorities that will improve the understanding of the population's biology and ecology throughout its range will contribute to more comprehensive management initiatives in all range states.

The Flyway Plan is undertaken within the guidelines of the recent *Agreement on the Conservation of African-Eurasian Migratory Waterbirds* (1995), known as the AEWA. This convention encourages the range states (in this case Norway, which includes Svalbard, and the

United Kingdom) to coordinate measures to ensure a favourable conservation status for the Svalbard barnacle goose population. This population, which numbered 23,000 in 1997, ranks as the eleventh smallest goose population in the world (out of 59 total) and falls within the AEWa Category A, the category for species/populations with an unfavourable conservation status (i.e. endangered). Range states are obliged to apply a strict level of protection identified within Article III/2 of the AEWa. The AEWa also requires co-operating range states to develop single species action plans for such species. For species within Category A, range states should accord: (a) strict protection; (b) identify, protect and manage a network of suitable habitats; (c) implement remedial measures where human activities are concerned; (d) prepare emergency procedures in case of disasters; (e) support research and monitoring; and (f) raise public awareness and exchange information and results from the above actions.

This Flyway Plan attempts to incorporate these AEWa Action Plan requirements for this population. The full contents of the Flyway Plan is listed in Table 1 and the key sections are outlined below.

To summarise, this small population warrants continued protection and management because of its size and concentrated distribution, its vulnerability to severe natural and anthropogenic declines, and its close proximity with rural communities. The conservation and management of this goose population are the responsibility of the governments of the countries which support the population at different times of the year (Norway and United Kingdom). The highlights of the population's history are listed in Table 2 and outlined in the section below.

Background and current status

One of four *Branta leucopsis* populations, the Svalbard barnacle goose population lives in discrete breeding and wintering areas. Its distribution during winter comprise one of the smallest wintering ranges of any goose population in the world. The size of this population in early parts of this century is unclear. There are anecdotal reports of several thousand birds having been counted on

the Solway at the turn of the century. Langley Roberts (in Harrison 1974), writes, concerning barnacle geese, 'It is known that flocks of 10,000 occurred on the Blackshaw Bank in the 1880s, and at the beginning of the present century flocks of 6,000 at Caerlaverock were commonplace.' However, the origins of these birds are unknown. It is quite possible, or even likely, that before agricultural improvements in the Hebrides increased the available food there, birds of the Greenland population may have wintered on the Solway. Early reports suggest that in the 1800s barnacle geese arrived in Scotland from the northwest (suggesting a Greenland origin), whereas, from the early 1900s they also arrived from the northeast (suggesting a Svalbard origin).

Certainly, reports from Svalbard from the turn of the century, when the archipelago was well explored, suggest rather small numbers there at that time. It has been suggested that the Svalbard population was established comparatively recently from a few founders, probably of Siberian stock (Owen & Shimmings 1992). Although, brent geese *Branta bernicla hrota* were first recorded in 1596 in Svalbard, the earliest record of barnacle geese was not until 1858. The fact that bones found in Helgeland date back to 3460 B.P. may indicate a much earlier existence.

Discovery that barnacle geese from Svalbard wintered in Britain came from a series of expeditions to catch and ring the birds. Hugh Boyd, from the Wildfowl Trust, and Magnar Norderhaug, from the Norwegian Polar Institute, initiated a collaborative effort confirming that geese caught on the Solway were, indeed, ringed in Svalbard and vice versa (see Boyd 1963, 1964; Larsen & Norderhaug 1964; Norderhaug et al. 1965; Norderhaug 1970, 1984). The first ringing expedition was launched in summer 1962 by a group of students from Oslo University (Bang et al. 1963).

The barnacle goose population on the Solway declined in the early part of the century to only 300 in 1948, probably because their roost sites were disturbed during the war. The population responded to several conservation measures, beginning with protection from hunting in Britain in 1954 and in Svalbard in 1955. In 1957, Caerlaverock National Nature Reserve was established and the first full census on the Solway Firth found 1,000 barnacle geese. Numbers on the Solway Firth grew rapidly to 4,250 in 1963 and remained around that level for ten years. After the

Table 1. Contents – Conservation and management plan for the Svalbard population of barnacle geese.

Introduction			
Part 1: Description			
Chapter 1.1	Geographical range	2.1.2	Population
1.1.1	Geographic range	2.1.2.1	Historic interest
1.1.2	Summary description	2.1.2.2	Present day
Chapter 1.2	Species information	Chapter 2.2	Evaluation
1.2.1	Taxonomy	2.2.1	Criterion for evaluation
1.2.2	Morphology	2.2.1.1	Naturalness
1.2.3	Population size and distribution	2.2.1.2	Rarity (population size)
1.2.3.1	Age and sex structures	2.2.1.3	Fragility
1.2.3.2	Range and movement	2.2.1.4	Typicalness
1.2.3.3	Population structure	2.2.1.5	Recorded history
1.2.3.4	Census techniques	2.2.1.6	Relationship to national/international populations
1.2.4	Population dynamics	2.2.1.7	Potential value
1.2.4.1	Productivity	2.2.1.8	Intrinsic appeal
1.2.4.2	Adult survival and mortality	2.2.2	Identification/confirmation of important features
1.2.4.3	Behavioural strategies and decision rules for Barnacle Geese	2.2.3	The population in wider perspective and implications for conservation
1.2.4.4	Population expansion in perspective	2.2.4	Research needs and future studies
1.2.5	Diet	2.2.4.1	Minimum research and monitoring requirements
1.2.5.1	Vegetation community selection	2.2.5	Specified limits
1.2.5.2	Vegetation utilization (Faecal analysis)	2.2.6	Long term or ideal management objectives
1.2.6	Cultural	2.2.7	Summary of factors influencing the achievement of long term objectives
1.2.6.1	History of human perception/utilisation	2.2.8	Conservation and management constraints
1.2.6.2	Current status of human perception/utilisation	2.2.8.1	Remit and constraints of Flyway Plan partners
1.2.6.3	Past management in nature conservation	2.2.8.2	Review of current policies and management
Chapter 1.3	Ecological relationships and implications for conservation	Chapter 2.3	Operational objectives
1.3.1	Interactions with other species	2.3.1	Rationale and operational objectives
1.3.2	Plant/animal interactions		
1.3.3	Goose movements and distribution	Part 3. Action plan (prescription)	
1.3.4	Goose grazing and merse management (The Wildfowl and Wetlands Trust)	Chapter 3.1	Outline prescriptions
		Chapter 3.2	Project groups
		Chapter 3.3	Project register
1.3.5	Goose grazing and field management (The Wildfowl and Wetlands Trust)	Part 4. Bibliography	
		Chapter 4.1	Bibliography
Part 2: Evaluation			
Chapter 2.1	Conservation status of the Svalbard Barnacle Goose population and its habitats	Part 5. Appendices	
2.1.1	Habitats	Appendix 1	Overview of relevant Norwegian legislation for management of the Svalbard population of Barnacle Geese
2.1.1.1	Historic interest	Appendix 2	Internationally important numbers and conservation assessment for the Svalbard population of Barnacle Geese at sites throughout their range.
2.1.1.2	Present status of habitats		
2.1.1.2.1	Management status and community initiatives		
2.1.1.2.2	Conservation status exercise		

Table 2. Key events in the Svalbard population of barnacle geese.

3460	– B.P. earliest record of Barnacle Goose bones in Helgeland
1858	– Earliest record on Svalbard
1880	– Flocks of 10,000 occur on Blackshaw Bank, Caerlaverock
1900's	– Early – 6,000 at Caerlaverock far fewer in Svalbard
1948	– After prolonged exploitation only 300 remain on Solway Firth
1954	– Full protection in UK
1955	– Full protection in Svalbard
1957	– First complete census in UK: population of 1,000
1957	– Caerlaverock National Nature Reserve established
1962	– First ringing expedition in Svalbard
1963	– First rocket netting at Caerlaverock
1970	– Eastpark Farm, Caerlaverock established
1971	– Full protection throughout Norway
1973	– Svalbard bird sanctuaries established
1973	– Long-term study begins
1973	– Population surpasses 5,000
1975	– Use of Helgeland discovered
1980	– Use of Bear Island discovered
1983	– First Svalbard goose symposium
1984	– Population surpasses 10,000
1986	– First complete census in Helgeland
1994	– Barnacle Goose Pilot Management Scheme established
1995	– Population surpasses 20,000
1995	– First international Flyway Plan meeting
1995	– Merse Management Scheme established
1995	– Helgeland Local Management Schemes established
1997	– Second Svalbard goose symposium
1998	– Publication of Flyway Plan

establishment of The Wildfowl and Wetlands Trust's reserve at Caerlaverock (in 1970) and Bird Sanctuaries in Svalbard (in 1973), another increase occurred in 1978 to an unprecedented total of 8,800. Numbers have continued to rise since then, surpassing 10,000 individuals in 1984, albeit with four additional stable phases where numbers appeared to plateau: between 1981–1983, 1984–1986, 1988–1990 and 1991–92. During the study period the population appeared to have experienced six brief phases of stability (ranging from 2–7 years) or steps prior to further expansion. A record number of barnacle geese were counted at the end of the wintering period on the Solway Firth in 1996–97, 23,000 individuals.

Review of current protection policies and management

The Svalbard population of barnacle geese is one of the most protected and well-managed waterfowl populations in Europe. Its celebrated recovery from a low of 300 birds to the current population of 23,000 is largely the result of effective conservation and management action. The geese are currently not hunted in any part of the population's range and the majority of haunts are within protected areas, many of which are managed specifically for providing optimal goose forage.

The information in Table 3 indicates that effective policies are in place throughout the birds' range. However, there is a great opportunity to establish programmes with 'International links between schools' and 'Twinning between sites' among countries. Such community education schemes could enhance the achievement of conservation and management objectives outlined in the plan.

The population in wider perspective and implications for management

All four barnacle goose populations have increased to unprecedented levels (Madsen et al. 1999). In 1996–97, the four populations amounted to 316,000 geese. The Svalbard population is the third largest numbering 23,000. There is some degree of interchange between the populations (Black et al. unpublished data), but the extent and significance of gene flow among populations needs clarification. The possibility of a decline in genetic diversity for the species as a whole, should the Svalbard population go extinct, is open to debate in the fields of conservation biology and population genetics.

Many goose populations throughout the world have proliferated to unparalleled status. In North America this was due to enhanced agricultural techniques and longstanding wildlife management policy aimed at providing optimal numbers of birds for hunting throughout their range (Ankney 1996). In Europe, it was due to the geese exploiting new winter food sources and a decline in hunting pressure (Ebbinge 1991; Owen & Black 1991; Madsen et al. 1999). As geese reach the carrying capacity of their natural habitats, sub-

Table 3. Summary of current major policies affecting the Svalbard population of barnacle geese. Notation: yes = activity occurring in most or all years, some = limited activity or activity in some years only, none = no activity occurring, n/a = not applicable.

	Flyway	Svalbard	Bjørnøya	Scotland	England	Helgeland
<i>Habitats</i>						
Site protection	yes	yes	pending	yes	yes	pending
Site management	some	none	none	yes	yes	yes
Monitoring use of protected sites	some	some	n/a	yes	some	n/a
Promotion of appropriate agricultural policies	some	n/a	n/a	some	some	some
Policies to reduce potential agricultural conflicts	yes	n/a	n/a	yes	n/a	yes
<i>Population and research</i>						
Development and maintenance of population model using data from projects listed below	yes	n/a	n/a	n/a	n/a	n/a
Regular population census and monitoring	some	some	some	yes	yes	some
Aerial census as appropriate	some	n/a	n/a	none	none	some/once
Continued capture and marking of geese	some	yes	none	yes	some	some
Co-operative ringing programme: resightings	yes	yes	yes	yes	some	yes
Encourage research and conservation initiatives	yes	yes	yes	yes	yes	yes
<i>International cooperation</i>						
Regular meetings to discuss international monitoring	twice	twice	twice	twice	twice	twice
Information exchange on site management, etc.	twice	n/a	n/a	twice	twice	twice
International cooperation in personnel training	none	none	none	none	none	none
<i>Legal status</i>						
Protection in all areas and periods	yes	yes	yes	yes	yes	yes
<i>Education</i>						
Hunter identification skills	some	some	some	some	some	some
Hunter education	some	some	some	some	some	some
International links between schools, etc.	none	none	n/a	none	none	none
Opportunities for site twinning programme	yes	yes	yes	yes	yes	yes
<i>International obligations</i>						
Compliance with relevant EEC Directives	yes	n/a	n/a	yes	yes	n/a
Ramsar Convention: wise use of wetlands etc.	yes	yes	n/a	yes	yes	n/a
AEWA (1995) Bonn Convention compliance	yes	yes	yes	yes	yes	yes

populations have established in entirely new localities, as in the case of the Baltic barnacle geese (Larsson et al. 1988; Larsson & Forslund 1994; Larsson & van der Jeugd 1998, this volume). Other populations, such as the lesser snow geese *Anser c. caerulescens* at La Pérouse Bay and other areas in Canada, destroy fragile habitats on which they depend through persistent grubbing and trampling action while foraging (Williams et al. 1993; Cooke et al. 1995).

To alleviate problems caused by growing numbers of geese, it may soon behove wildlife

managers to instigate proactive wildlife policy that protects key ecosystems and discourages further population expansion. Such notions, including the reopening of hunting geese for the market, are currently being discussed in North America with the aim of revising waterfowl management policy for the next century (Ankney 1996). In Britain and Norway, hunting geese for sport and/or management is an issue of continued dialogue (Kear 1990; Directorate for Nature Management 1996; Scottish Office 1996; Madsen 1997).

Review of important features

Through prolonged exploitation the population fell to 300 birds in 1948. The current conservation measures in effect in Norway reflect the need to protect goose populations in the Arctic, especially during the breeding season. In Svalbard particular measures were implemented to protect the geese from over-harvesting in summer, including the ban on harvesting since 1955 and the establishment of disturbance-free Bird Sanctuaries in 1973. In Scotland protective measures were also taken by banning hunting since 1954, establishing a large refuge out of the birds' traditional salt marsh foraging area in 1957 and managing pastures and merses at The Wildfowl and Wetlands Trust at Caerlaverock specifically for goose grazing during the non-breeding season, beginning in 1970. Having responded to these conservation strategies, the population has recovered to 23,000 in 1997.

The Svalbard population of barnacle geese is still bound to traditional mudflats (roosts) and salt marshes (merses), many of which were indirectly managed for the geese through farming activities for hundreds or even thousands of years. The geese use a total of c. 75 key sites that are under various jurisdictions throughout their range (including about 35 farms and large areas of coastal marsh). Several of these small sites can hold more than 50% of the population which puts the population at severe risk. Many of these are protected and managed specifically for the geese, with the notable exceptions of Nordenskiöldkysten, all Bjørnøya sites and many sites in Helgeland.

In Scotland the geese provide one of the spectacles that locals and tourists savour. In Svalbard, the image and lifestyle of the barnacle goose is synonymous with wilderness values, which is very much a part of the Norwegian culture. The conservation success story of the Svalbard barnacle goose population is referred to widely and recognised as a key example for wildlife managers throughout the world.

Research needs and future studies

Through a wide ranging research programme, initiated by The Wildfowl and Wetlands Trust and

yielding over 100 scientific publications, scientists and managers have been striving towards a fuller understanding of all aspects of the population's biology and ecology throughout its range. This programme has encouraged the development of the Flyway Plan which addresses conservation and management problems affecting the population at an international level and facilitates cooperation among countries responsible for the well-being of this small population (Norway and the United Kingdom). The Directorate for Nature Management views the Svalbard barnacle goose population as a 'reference species' with unique scientific value. The history of the population demonstrates successful nature conservation in action. The vast bank of knowledge from barnacle goose research can be used in the design of management schemes for a variety of populations (Directorate for Nature Management 1996).

Research required to service the aims of the Flyway Plan can be viewed at two levels: basic monitoring and proactive investigation. Basic monitoring is relatively straight forward. It involves assessing population size, mapping the distribution of flocks and habitat types, and determining population parameters, such as percentage of juveniles, brood sizes and survival. Such monitoring at appropriate stages of the lifecycle provides managers with a broad set of information on which decisions can be based.

Proactive investigation also provides managers with a sound understanding of the mechanisms and processes that are involved in the population's behaviour. Through carefully designed research, managers will be better able to assess the animal's response to various management initiatives. This work focuses on individually marked birds and their environment (habitat requirements, plant-animal interaction, predation risk, etc).

By working with the Svalbard barnacle goose population, managers have the opportunity to build on information from both types of research. Previous work has indicated that some segments of this population (i.e. some colonies) are showing signs of density dependent effects, through decreased productivity, survival, growth rates and adult body size. We suspect that this is a function of increased competition for a limited food resource on the breeding grounds (i.e. our working hypothesis). However, the population as a whole appears to be increasing in a stepwise fashion.

The current increase can be the result of

recruitment from (1) new and previously unknown colonies, (2) old colonies are periodically released from density dependence, perhaps through a revitalize food source or a lessening of predation risk, (3) birds that utilise newly colonised spring staging sites, and/or (4) birds that utilise the new and improving segments of the wintering grounds (i.e. new refuges and salt marsh).

Clearly, we have a long way to go before we fully understand the functional and behavioural responses that drive the distribution and dynamics of this population. There are three developments in the recent history of the Svalbard barnacle goose that need attention. To better plan future management initiatives we need to assess what impact the following natural and anthropogenic events may have on the population: (a) the effect of increased density of birds in Svalbard, e.g. the development of satellite colonies, the mechanism behind the fluctuating productivity of established colonies, and the response of arctic vegetation to persistent goose grazing; (b) the 'managed' distribution of foraging flocks during winter by the Goose and Merse Management Schemes, and the Countryside Stewardship Scheme in the U.K.; and (c) the 'managed' distribution of foraging flocks during spring by the Coastal Local Management and Sheep Translocation Schemes in Norway.

Further research on population expansion issues will provide information about the well-being and future growth of the population. Research that discovers how and why the birds respond to the new management regimes will help in the assessment and fine tuning of those initiatives. Both lines of research are inseparable since the population's behaviour will determine the type and extent of management that is required.

The research required to service the aims of the Flyway Plan are listed in PART 3 – ACTION PLAN (Prescription), under Chapter 3.1 Outline prescriptions, Operational Objectives 7 to 10 (see below).

Minimum research and monitoring requirements

The lowest level of research and monitoring needed to service the Flyway Plan is described below. The term monitoring includes the process

of data scrutiny and the preparation of management recommendations:

Maintain a monitoring programme to track future numbers and distribution in (a) Svalbard, (b) Bjørnøya, (c) the Solway Firth, (d) Helgeland, and (e) additional areas as and when they occur.

Maintain a monitoring programme on the wintering grounds to assess future population parameters (numbers, proportion of young, brood size/single goslings).

Maintain a monitoring programme to assess and refine existing and possible future management schemes on a) the Solway Firth, and b) in Helgeland.

Specified or alert limits

This section identifies a set of objective criteria that will alert managers that a potentially negative change in population has occurred. When the limit is reached, managers should be prepared to increase their effort to identify the reasons behind the change. On deciding that the decline is serious, the Flyway Plan partners should be consulted. Similar considerations are to be made in the event of further growth in the population size.

Lower limits

A revealing method for determining the well being of a population is to review the trend in estimated population sizes. Because of its manageable size and accessibility during winter, this type of data is available for the Svalbard barnacle goose population.

Simulated population values are derived using a stochastic density independent population growth model from a starting population of 17,770 (the 5-year mean up to 1996), using known variability in population growth rate over the last 35 years. The degree of acceptable change is a matter of personal and/or political opinion. For this reason a range of values is presented for consideration.

Thus, assuming conditions which have applied over the last 35 years will continue over the next 10 years, there is, for example, a 5% chance that the population will drop below 14,600, a 1% chance it will drop below 12,000, or a 0.1%

Table 4. Probability of population reduction in the next 2, 5 and 10 year periods; starting with a population of 17,770.

Probability	One simulation in:	Approximate minimum expected population size within:		
		2 years	5 years	10 years
0.0001	10,000	10,600	8,600	7,100
0.001	1,000	11,600	9,300	9,000
0.01	100	12,900	12,000	12,000
0.05	20	14,600	14,600	14,600
0.1	10	15,700	15,700	15,700
0.25	4	17,200	17,200	17,200

chance it will drop below 9,000 (Table 4). Clearly, considering a longer time span, there is more chance that the population will decline by a greater amount, at least for the lower probability levels.

It is suggested, therefore, that when the population is reduced to fewer than 12,000 for five years (or the five year mean is less than 12,000), an enhanced attempt to (a) pinpoint the cause should be made (e.g. whether through a decline in reproduction and/or survival and/or emigration), (b) review the relative priorities (e.g. Highly Desirable or Desirable) in Part 3: the Action Plan, and (c) consider whether further initiatives are required.

This level is equivalent to a reduction in numbers once in 100 years that may be expected through natural fluctuations under current conditions. If the population drops to this level, it is liable to bounce back in the following year or two; but if this level is maintained for a number of years, it is likely to be due to a long-term effect rather than natural fluctuations. Therefore, in the fifth year at this level, action should be taken.

Managers should also be aware of the potential impact of any policy changes in agriculture, land reclamation, mineral exploitation, pollution, hunting or any other cause of major disturbance likely to effect any of the traditional goose haunts in the population's range.

Cautionary note: This model is based on population data obtained through 1996 and data from individual birds through 1995. With time the functional and behavioural responses that drive the distribution and dynamics of this population may change, thus necessitating the formulation of a revised population model.

Population expansion

Based on the current population parameters it appears that certain segments of the population are currently being limited through reduced productivity and survival. This effect was first recorded when there were 8,000 to 10,000 individuals in the population (Pettifor et al. 1998, this volume). Other segments of the population do not appear to be limited and numbers which return to the wintering grounds continue to increase in a step-wise fashion. The population in 1997 was 23,000 individuals.

The AEW (1995: Bonn Convention) considers populations of less than 25,000 to be under threat. The Convention does not recommend/encourage hunting goose populations of fewer than 100,000.

However, given the small range of the Svalbard barnacle goose population and its close proximity to rural communities, continued expansion of the population is likely to result in the colonisation of new locations that are not included in current management initiatives that are aimed at reducing potential conflict with the agricultural community.

It is suggested, therefore, that when the population surpasses 25,000 (i.e. five year mean is greater than 25,000), an enhanced attempt to (a) pinpoint the cause should be made (e.g. whether through increased reproduction and/or a decrease in mortality and/or immigration), (b) review the relative priorities (e.g. Highly Desirable or Desirable) in Part 3: the Action Plan, and (c) consider whether further initiatives are required.

Long-term or ideal management objectives

It is important to distinguish between long-term objectives and shorter term obtainable or 'operational' objectives. The process begins with defining the long-term objectives. Next, all constraints and trends which may influence the achievement of long-term objectives are identified.

For migratory waterfowl in Europe, the Bonn Convention provides the guidelines for these ideal objectives. Managers should keep in mind that management strategies for the Svalbard barnacle goose population may affect the conservation status of other species. There may be protected sites, or parts of sites, used by the geese where conservation priorities may need to be targeted for other fauna or flora. The potential for interaction between species and management strategies should be considered in all cases. Conflicting conservation priorities should be avoided by site managers.

The following long-term objectives have been identified:

1. To maintain favourable conservation status for the Svalbard barnacle goose population throughout its geographical range. The conservation status of the population will be taken as favourable when:

- population parameters indicate that it is maintaining itself on a long term basis as a viable component of its natural habitat; the population should number at least 25,000 individuals,
- the natural range of the population is neither being reduced nor is likely to be reduced in the foreseeable future, and through habitat management, there is potential for reoccupation of formerly utilised sites,

- there is, and will probably continue to be, sufficiently large areas of habitat to maintain the population on a long term basis.

2. To encourage and support coordinated and collaborative research and monitoring of the population throughout the range states.

3. To raise public awareness of the conservation status of the population throughout the range states.

The Action Plan: outline for the future

The following section outlines the 14 key, operational objectives followed by the prescriptions that outline the first steps toward identifying the total work required to fulfil the objectives. Prescriptions are ranked as Highly Desirable or Desirable, thus giving managers some guidance in assigning priorities. Those ranked as Essential are required by national or international law. The lead Flyway partner is indicated for each prescription. The term 'NGOs' refers to Non Governmental Organisations.

POPULATION PROTECTION AND MANAGEMENT

1. To maintain and implement necessary protection of breeding, moulting and staging barnacle geese in Norway.

1.1 *Svalbard: Maintain existing protective legislation for barnacle geese while on the breeding and moulting areas in Svalbard. Highly Desirable (Lead: Governor of Svalbard)*

1.2 *Bjørnøya: Maintain existing protective legislation for barnacle geese while on Bjørnøya. Highly Desirable (Lead: Governor of Svalbard)*

1.3 *Helgeland: Maintain existing protective legislation for the species while in Helgeland. Highly Desirable (Lead: County Governor of Nordland)*

2. To maintain and implement necessary protection of wintering barnacle geese on the northern and southern shores of the Solway Firth.

2.1 *United Kingdom: Maintain existing protective legislation for the species while on feeding and roosting areas in the UK. Highly Desirable (Lead: Scottish Natural Heritage, English Nature, Joint Nature Conservation Committee)*

2.2 *Scotland: Monitor and assess levels of illegal shooting of wintering barnacle geese on the northern coast of the Solway Firth. Desirable (Lead: Scottish Natural Heritage).*

SITE PROTECTION AND MANAGEMENT

3. To maintain and implement protection of a network of key habitats for prebreeding, breeding, moulting, post-breeding in Svalbard, autumn staging geese on Bjørnøya, and spring staging geese in Helgeland. If necessary expand the current areas of protection to include additional key sites.

3.1 *Svalbard. Maintain necessary protection of existing Bird Sanctuary areas and practice a strict regulation of tourism and other activities in all protected and other sensitive areas. Highly Desirable (Lead: Governor of Svalbard)*

3.2 *Svalbard: Consider extending the Bird Sanctuary network to include other key colonies, moulting areas [such as Nordenskiöldkysten] and areas used as pre- and post-breeding staging sites. Desirable (Lead: Governor of Svalbard)*

3.3 *Bjørnøya: Complete the process to establish site*

protection for Bjørnøya with nature reserve status. *Highly Desirable* (Lead: Directorate for Nature Management)

3.4 *Helgeland*: Complete the process to establish site protection for key foraging and roosting areas in Helgeland. *Highly Desirable* (Lead: Directorate for Nature Management, County Governor of Nordland)

3.5 *Nordland*: Compile and implement local habitat management plans for key sites in Helgeland. *Highly Desirable* (Lead: County Governor of Nordland)

4. To maintain and implement protection of sufficient suitable habitat at existing key feeding and roosting areas on the northern and southern coasts of the Solway Firth. If necessary expand the current areas of protection to include additional key sites.

4.1 *Solway Firth*: Maintain necessary protection of existing statutory designated conservation areas and key foraging and roosting areas throughout the Solway Firth. *Essential* (Lead: Scottish Natural Heritage, English Nature)

4.2 *Solway Firth*: Maintain and/or enhance management of existing statutory designated conservation areas and other foraging and roosting sites. *Essential* (Lead: Scottish Natural Heritage, English Nature)

4.3 *North Solway Firth*: Consider extending SPA and SSSI network to include key sites that are currently not included in the network (i.e. Longbridgemuir). *Desirable* (Lead: Scottish Natural Heritage)

4.4 *Solway Firth*: Compile and/or implement site-based habitat management plans for statutory and NGO reserves. *Highly Desirable* (Lead: Scottish Natural Heritage, and relevant NGOs)

5. To lessen potential conflict between the population and agricultural interests on the Solway Firth.

5.1 *Solway Firth*: Maintain, refine and if necessary, extend goose management scheme on farmland; i.e. Goose Management Scheme. *Highly Desirable* (Lead: Scottish Natural Heritage)

5.2 *Solway Firth*: Maintain, refine and, if necessary, extend habitat enhancement schemes on traditional feeding sites, i.e. the Merse Management and Countryside Stewardship Schemes. *Highly Desirable* (Lead: Scottish Natural Heritage, English Nature)

5.3 *Solway Firth*: Liaise closely with farmers in areas of potential conflict to advise on management options. *Highly Desirable* (Lead: Scottish Natural Heritage, English Nature)

5.4 *Solway Firth*: Liaise where appropriate, with the National Goose Forum in Scotland over management issues and agricultural conflict. *Highly desirable* (Lead: Scottish Natural Heritage, and relevant NGOs)

6. To lessen potential conflict between the population and agricultural interests in Helgeland (Nordland).

6.1 *Nordland*: Maintain, refine and, if necessary, extend existing goose management scheme near farmland; i.e. Coastal Grazing Scheme. *Highly Desirable* (Lead: County Governor of Nordland)

6.2 *Nordland*: Liaise closely with farmers in areas of potential conflict to advise on management options through

local management plans. *Highly Desirable* (Lead: County Governor of Nordland)

6.3 *Nordland*: Maintain, refine and, if necessary, extend habitat enhancement schemes on traditional feeding sites. *Desirable* (Lead: County Governor of Nordland).

MONITORING AND RESEARCH

7. Population expansion issues: Maintain the high scientific value of the Svalbard barnacle goose population by investigating mechanisms behind and the consequences of increased density of birds in Svalbard, e.g. the development of satellite colonies, the mechanism behind the fluctuating productivity of established colonies, and the response of arctic vegetation to persistent goose grazing.

7.1 *Solway Firth*: Maintain a monitoring programme on the wintering grounds to assess population parameters (e.g. population size and proportion of young). *Highly Desirable* (Lead: Scottish Natural Heritage, and relevant NGOs)

7.2 *Svalbard*: Maintain a monitoring programme to track numbers and distribution at key sites in Svalbard. *Highly Desirable* (Lead: Norwegian Polar Institute, Governor of Svalbard)

7.3 *Svalbard*: Establish a long-term monitoring scheme and a supporting experimental programme to detect changes in goose-plant interactions at key sites in Svalbard; particularly any serious degradation of habitats. *Desirable* (Lead: Norwegian Polar Institute, and relevant NGOs)

7.4 Identify which birds are responsible for the growth in the population, their attributes and habitats. *Desirable* (Lead: Norwegian Institute for Nature Research, and other relevant NGOs)

7.5 Fine tune and finalise predictive population models. *Desirable* (Lead: Scottish Natural Heritage, and relevant NGOs)

7.6 Investigate the proximate factors that are responsible for the density dependent decline in reproductive and survival parameters, namely the interaction between the geese themselves (social regulation, kin selection) and their food plants (foraging ecology and long-term plant phenology). *Desirable* (Lead: relevant NGOs)

7.7 Determine the population consequences of site fidelity and colonization of new sites in Svalbard. *Desirable* (Lead: relevant NGOs)

7.8 Determine the mechanisms behind explorative behaviour that leads to expansion to new winter feeding areas, staging areas and nesting sites, i.e. inland expansion or short-stopping. *Desirable* (Lead: relevant NGOs)

7.9 Determine the occurrence and significance of real or potential gene flow between and within barnacle goose populations. *Desirable* (Lead: relevant NGOs)

8. *Solway Firth*: Investigate mechanisms and consequences of the 'managed' distribution of foraging flocks during winter by Goose and Merse Management Schemes, and the Countryside Stewardship Scheme.

8.1 Maintain a monitoring programme to assess and refine management schemes. *Highly Desirable* (Lead: Scottish Natural Heritage, English Nature)

8.2 Determine the population consequences of site fidelity and colonization of new sites on the Solway Firth. *Desirable* (Lead: relevant NGOs)

8.3 Determine the extent to which the geese rely on nutrients from the salt marsh food versus carbohydrates from agricultural pastures in order to determine the relative impact of the Goose and Merse Management Schemes. *Desirable* (Lead: Scottish Natural Heritage, English Nature, and relevant NGOs)

8.4 Through experimental design quantify the precise farming regimes that will yield optimal forage for the geese on pastures and merses at designated refuges, information that will lead to increased goose usage and improved value for management money. *Desirable* (Lead: Scottish Natural Heritage, English Nature, and relevant NGOs)

9. Helgeland: Investigate mechanisms and consequences of the 'managed' distribution of foraging flocks during spring by Coastal Grazing and Sheep Translocation Schemes.

9.1 Maintain a monitoring programme to assess and refine management schemes in Helgeland. *Highly Desirable* (Lead: County Governor of Nordland)

9.2 Determine the population consequences of site fidelity and colonization of new sites in Helgeland. *Desirable* (Lead: County Governor of Nordland, and relevant NGOs)

9.3 Determine the extent to which the geese rely on nutrients from the salt marsh food versus carbohydrates from agricultural pastures in order to assess the relative impact of the Coastal Grazing and Sheep Translocation Schemes. *Desirable* (Lead: relevant NGOs)

10. Migration and inter-specific interaction issues: investigate the causes and constraints during migration and the potential conflict between species using the same habitats.

10.1 Identify the location and significance of pre-breeding staging sites (in May) in Svalbard. *Highly Desirable* (Lead: Norwegian Polar Institute, Norwegian Institute for Nature Research)

10.2 Identify the location and significance of post-breeding, pre-migration staging sites (in August–September) in Svalbard. *Desirable* (Lead: Norwegian Polar Institute, and relevant NGOs)

10.3 Establish the significance of vegetation to the geese that stage on Bjørnøya on the autumn migration. *Desirable* (Lead: Norwegian Polar Institute)

10.4 Quantify the potential inter-specific competition between barnacle geese and other herbivores, e.g. light-bellied brent, common eider and reindeer in Svalbard. *Desirable* (Lead: Norwegian Polar Institute, and relevant NGOs).

COLLABORATION

11. To create an international review panel to initiate, oversee and review Flyway Plan.

11.1 Identify Flyway Plan coordinator to oversee implementation of monitoring and research programme. *Highly Desirable* (Lead: Directorate for Nature Management, Scottish Natural Heritage)

11.2 Identify review panel members and initiate periodic meetings to effectively oversee and review the Flyway Plan. *Highly Desirable* (Lead: Directorate for Nature Management, Scottish Natural Heritage)

12. To create a forum for advice and information exchange between all range states concerning monitoring, research, training, education & management.

12.1 Initiate periodic meetings to facilitate general information exchange. *Desirable* (Lead: Directorate for Nature Management, Scottish Natural Heritage)

12.2 Identify research needs and assign lead organisations to coordinate and implement research programmes throughout the range states. *Desirable* (Lead: Directorate for Nature Management, Scottish Natural Heritage)

13. To create and establish a joint and free access to relevant data from monitoring and research on the species throughout the flyway, to both range states and non-governmental organisations.

13.1 Describe and document existing data and databases occurring at governmental and non-governmental agencies. *Highly Desirable* (Lead: Directorate for Nature Management, Scottish Natural Heritage)

13.2 Establish all data and updated information in pre-designed databases, and identify lead organisations to run databases for all interested parties. *Highly Desirable* (Lead: Directorate for Nature Management, Scottish Natural Heritage)

13.3 Ensure that all future data collected are according to research needs, are collected and stored as outlined, and are made available to all interested parties. *Desirable* (Lead: all agencies).

AWARENESS AND EDUCATION

14. To raise awareness of conservation issues impacting on the population amongst sectors of public within all range states.

14.1 Raise awareness of the potential effects of recreational disturbance to geese throughout their range. *Highly Desirable* (Lead: all agencies)

14.2 Liaise closely with farmers and agricultural agencies over goose conflict situations and management options. *Desirable* (Lead: Directorate for Nature Management, Scottish Natural Heritage, County Governor of Nordland).

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Areas in Svalbard important for geese during the pre-breeding, breeding and post-breeding periods

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The barnacle goose *Branta leucopsis* has shown the largest change in the breeding distribution among geese in Svalbard during the recent decades. The expansion of the breeding distribution has coincided with the increase in the population size. The changes in the breeding distributions in Svalbard of brent geese *Branta bernicla* and pink-footed geese *Anser brachyrhynchus* appear to have been small, although the knowledge of the total breeding distributions in Svalbard of these two species is incomplete.

Some pre-breeding staging areas for geese in Svalbard have been located. South-facing, snow-free slopes in coastal regions of western Spitsbergen seem to be areas frequently used by geese before they reach their breeding localities.

Post-breeding concentrations of geese have been found over most of the coastal regions of the archipelago. Most barnacle geese leave their nesting islands just after hatching and raise their goslings in coastal tundra areas rich in small lakes and lush vegetation. The largest numbers of barnacle geese during this period are found along the western coasts of Spitsbergen from Isfjorden to Sørkapp. The largest aggregations of brent geese have been recorded in coastal regions in northern and southeastern parts of the archipelago and at Sørkapp, whereas important post-breeding aggregations of pink-footed geese have been located in coastal regions in northern, central and southern parts of Spitsbergen, as well as in southeastern Svalbard. It is not known to what extent the geese fly to specific pre-migratory staging areas before they start their autumn migration from Svalbard. Recent satellite-telemetry studies indicate that such areas are used at least by parts of the populations.

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Introduction

Geese are important herbivores which graze of the tundra vegetation in coastal regions of Svalbard. Three goose species presently breed in Svalbard: the pink-footed goose *Anser brachyrhynchus*, the barnacle goose *Branta leucopsis*, and the brent goose *B. bernicla*. The population sizes of these three species as well as the breeding distributions have exhibited large variations. The changes may be partly attributed to environmental changes and management measures both in Svalbard and at wintering and migration staging sites. The current population sizes of these geese are given by Madsen et al. (1998, this volume). Proper management of these populations during their presence in Svalbard is dependent on detailed knowledge of their habitat use throughout the summer season as well as on data on the dynamics and development of sub-populations in different parts of the breeding areas.

The current management of the Svalbard goose populations enforced by the Norwegian government is based on a national goose management strategy (Directorate for Nature Management 1996; Bø et al. 1998, this volume). In addition goose management must take into consideration the recent Agreement on the Conservation of African-Eurasian Migratory Waterbirds (1995) under the terms of the Bonn Convention for migratory species. This agreement encourages the range states to co-ordinate efforts to enhance populations of waterbird populations of great conservational concern and to prepare a 'Flyway Conservation and Management Plan' to ensure a favourable conservation status for the population at a defined population size. The Svalbard barnacle goose and brent goose populations are regarded as such populations of great concern, and a 'Flyway Plan' for the Svalbard barnacle goose population has been prepared by the governments of Norway and the United Kingdom (Black 1998, this volume).

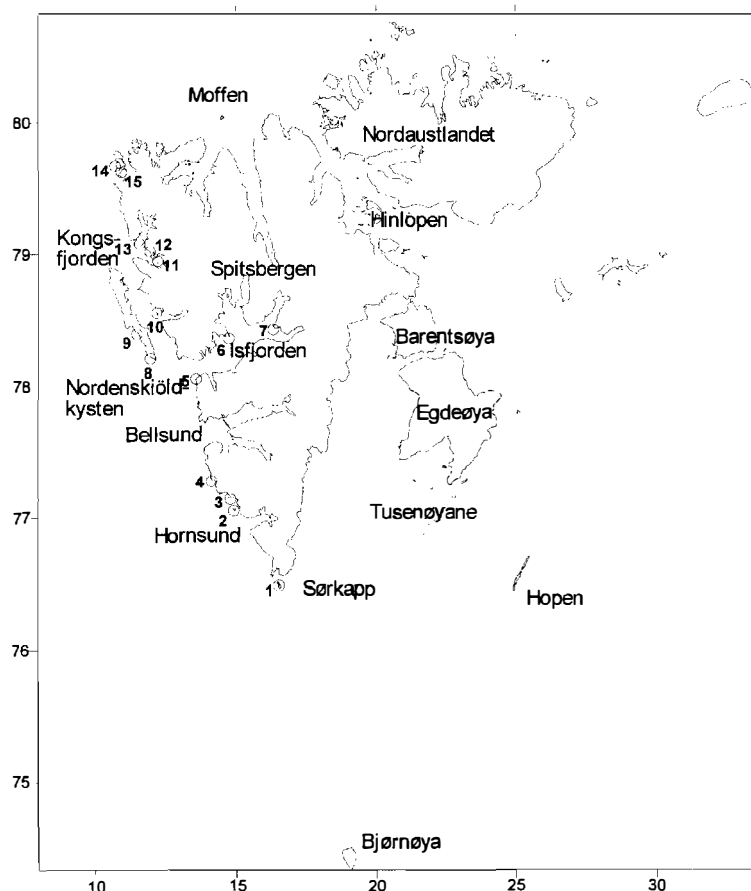


Fig. 1. Location map of Svalbard with major place names mentioned in the text. Numbers refer to bird sanctuaries (see Table 1).

In 1973 the Norwegian Government established 15 bird sanctuaries along the western coasts of Spitsbergen in order to protect important breeding areas of eiders and geese (Fig. 1). To assess the effects of this conservation measure for the development of the goose populations, censuses of breeding numbers have been made in the sanctuaries by the Norwegian Polar Institute (NP) and the Governor of Svalbard.

A status of the current knowledge of the Svalbard goose populations was presented through a collection of papers from an international goose symposium in 1983 (Mehlum & Ogilvie 1984). This collection includes a status of the goose populations in the bird sanctuaries in Svalbard (Prestrud & Børset 1984). Some additional information on the distribution and breeding colony sizes of geese in Svalbard has been published since then. An update on the

development of the number of breeding barnacle geese in the sanctuaries was given by Prestrud et al. (1989), whereas Persen (1986) and Bustnes et al. (1995) have documented the breeding numbers and distribution of brent geese in Tusenøyane.

This paper documents changes in breeding distribution of the three goose populations in Svalbard during the last decades based on the data available. It also summarises (1) the knowledge of the distribution of goose flocks in Svalbard between their arrival after spring migration and the initiation of breeding, and (2) the distribution of known habitats for moulting geese and areas of goose aggregations prior to autumn migration. Lastly, the paper presents the development of breeding numbers of barnacle geese from early 1980s to the present in the bird sanctuaries in Svalbard.

Materials and methods

Svalbard is a large territory comprising 63,000 km². The total length of the coastline is ca. 8,800 km. Most geese habitats are located along or near the coasts. It is a comprehensive task to survey the whole of Svalbard for geese, and the resources available are limited. Access to distant areas is constrained by sea ice during the first part of the summer.

Making visits to remote areas requires costly logistics (ship, helicopter, etc.). NP provided the opportunity to conduct bird surveys in the northern and eastern parts of Svalbard during some of their summer expeditions to these regions. With the use of helicopter to cover large parts of the coasts of northern and eastern Svalbard, we were able to make surveys of post-breeding flocks of waterfowl. Most visits to the northeastern areas (mainly Nordaustlandet) were made in August (after hatching of most geese).

The Governor's office, which compiles data concentrating on the bird sanctuaries, also provides important goose data. In 1997 the office was instrumental in a survey in the Hinlopen Strait area, and in 1985 and 1995 it conducted goose surveys in Tusenøyane (Persen 1986; Bustnes et al. 1995).

Since the early 1980s, more detailed records of the population development in breeding barnacle geese have been obtained from the Kongsfjorden area, where several goose research groups have been working (Univ. Groningen, NINA, NP). Another important, long-term data set on habitat use by barnacle geese is that obtained by R.H. Drent and co-workers at Nordenskiöld kysten (Drent et al. 1998, this volume).

Important data on brent geese and barnacle geese at Tusenøyane were obtained in 1987 and 1989 by researchers from the Danish National Environment Research Institute in collaboration with NP (Madsen et al. 1989; Bregnballe & Madsen 1990; Madsen et al. 1992).

Helicopter surveys

The aerial surveys of post-breeding geese were carried out by two trained observers from a Bell 206 or a Aerospatiale Ecureille AS350 helicopter

flying at an altitude of 100–200 feet and at a speed of about 60–80 knots. The helicopter was usually positioned 20–50 m off the coastline. Discriminating was not made between young and adult individuals.

The following coastal sections were covered: Tusenøyane, 18 Aug. 1982, 1–5 Aug. 1985, 22–23 July 1989, 26 July 1992; Edgeøya, 5 and 11 Aug. 1989, 22 July (Negerpynten–Kvalpynten), and 26 July 1992 (Kapp Lee-Årdalsnuten); Barentsøya, 10–11 Aug. 1989 (Dunérbukta–Sundneset), 26 July 1992 (Mistakodden–Sundneset); Northern Spitsbergen, 15 Aug. 1989 and 28–29 Aug. 1990.

Data presentation and limitations

In this paper the observations of geese are divided into three periods: the pre-breeding period, defined as 1 May–7 June; the breeding period, 16 June–31 July; and the post-breeding, 1 August–31 September.

The maps in this paper have been generated from published data and from the bird database maintained by the Norwegian Polar Institute. Data are scarce from many parts of Svalbard, and many of the observations included in the database originate from occasional and short visits. Because of limitations in data availability from many regions in Svalbard, interpretations of the distribution maps presented should be made with care. However, this paper demonstrates the usefulness of occasional bird observations reported by people travelling in remote parts of the archipelago.

The recent results derived from satellite telemetry studies on brent geese (Clausen & Bustnes 1998, this volume) and barnacle geese (Butler & Woakes 1998, this volume) are not included in this presentation.

Results

Breeding distribution

Brent goose

The locations of all reported breeding localities of

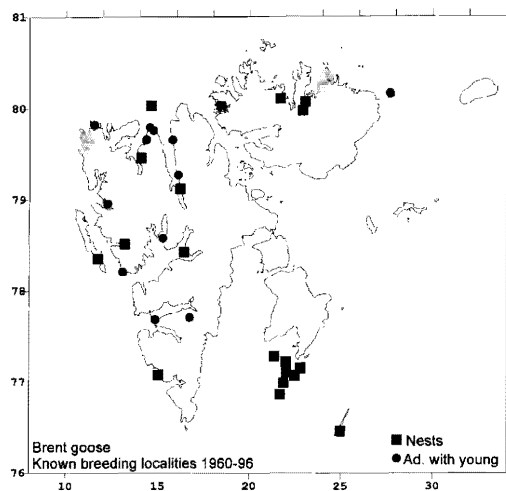


Fig. 2. Breeding distribution of brent geese *Branta bernicla hrota* in Svalbard 1960–1996.

brent geese in the period 1960–96 are presented in Fig. 2. The map includes known nest locations and observations of families with goslings. The breeding localities of the brent goose cover most regions in the archipelago. However, the majority of the numbers of breeding pairs is confined to two areas, Tusenøyane and Moffen. In 1993 a total of 43 nests were recorded on Moffen, whereas the number of breeding pairs in Tusenøyane was estimated at 435–600 in 1985 (Persen 1986). At the other breeding localities the number of nests found ranged from 1 to 18. The data available on breeding brent geese are too scarce for making any conclusions about changes in the breeding distribution pattern in the period from 1960 to present.

Barnacle goose

In concert with the increase in the Svalbard barnacle goose population in the second half of this century, a large expansion of the breeding distribution has been documented. According to Løvenskiold (1964) only five breeding colonies were known prior to 1960 (Fig. 3A). In addition, reports from various authors indicate that the species might breed at several other locations in various parts of western and northwestern Spitsbergen (Løvenskiold 1964).

Norderhaug (1970) summarised the breeding

distribution in the 1950s and 1960s (Fig. 3B). By then the number of breeding localities had increased to 11 and included a colony on Barentsøya in eastern Svalbard, a colony at Skorpa in northwestern Spitsbergen, and a single record of a family at Sparreneset in Nordaustlandet. The colony in Longyeardalen (Fig. 3A) apparently disappeared before 1931 (Løvenskiold 1964).

The rapid breeding expansion during the 1970s and 1980s resulted in new colonies being established along the western coasts of Spitsbergen from Sørkapp to northwestern Spitsbergen (Fig. 3C). A colony was also recorded in Tusenøyane in southeastern Svalbard. The expansion continued into the 1990s. The changes in breeding distribution from the early 1980s include a further expansion in northwestern Spitsbergen, to the fjords of western Spitsbergen, and in Tusenøyane, as well as the establishment of three small new colonies in the Hinlopen Strait area. The breeding distribution in the 1980s and 1990s is illustrated in Fig. 3D.

Most of the barnacle goose population now breeds on islands, but some of the population is known to breed in colonies on inland cliffs. The oldest colony, which was situated in Longyeardalen, Isfjorden, became extinct before 1931. In the inner part of Isfjorden, the species is known to breed in three areas in close proximity: Fjordnibba (5 pairs 1987), Nøisdalen (1 nest 1995), and Sassendalen (Prestrud et al. 1989; Mitchell et al. 1998, this volume). Up to 100 pairs may breed in Sassendalen (Prestrud et al. 1989). In Reindalen barnacle geese have been found breeding on high cliffs at five different locations (Jacobsen 1994). A total of 53 pairs bred in 1990 (Sveum & Hoddø 1990) and 50 pairs in 1994 (Jacobsen 1994). A small breeding colony is located in the southwestern part of Barentsøya, where 7 nests were found in 1969 (De Korte 1972), and 11 pairs in 1983 (Prestrud unpubl.). A small fraction of the expanding colony in Kongsfjorden also breeds at inland colonies, nesting regularly within the village of Ny-Ålesund (Tombre et al. 1998, this volume) and at the cliff Stuphallet on Brøggerhalvøya (1 pair in 1996, Mehlum unpubl.).

The breeding numbers of barnacle geese in the bird sanctuaries in Svalbard have been assessed at various times during the period 1982 to 1996 (Table 1). Kapp Linné Bird Sanctuary was not included in the table as only 1–3 pairs of barnacle geese had been reported breeding there in 1996 and 1997 (G. Bangjord pers. comm.). In 1995, the

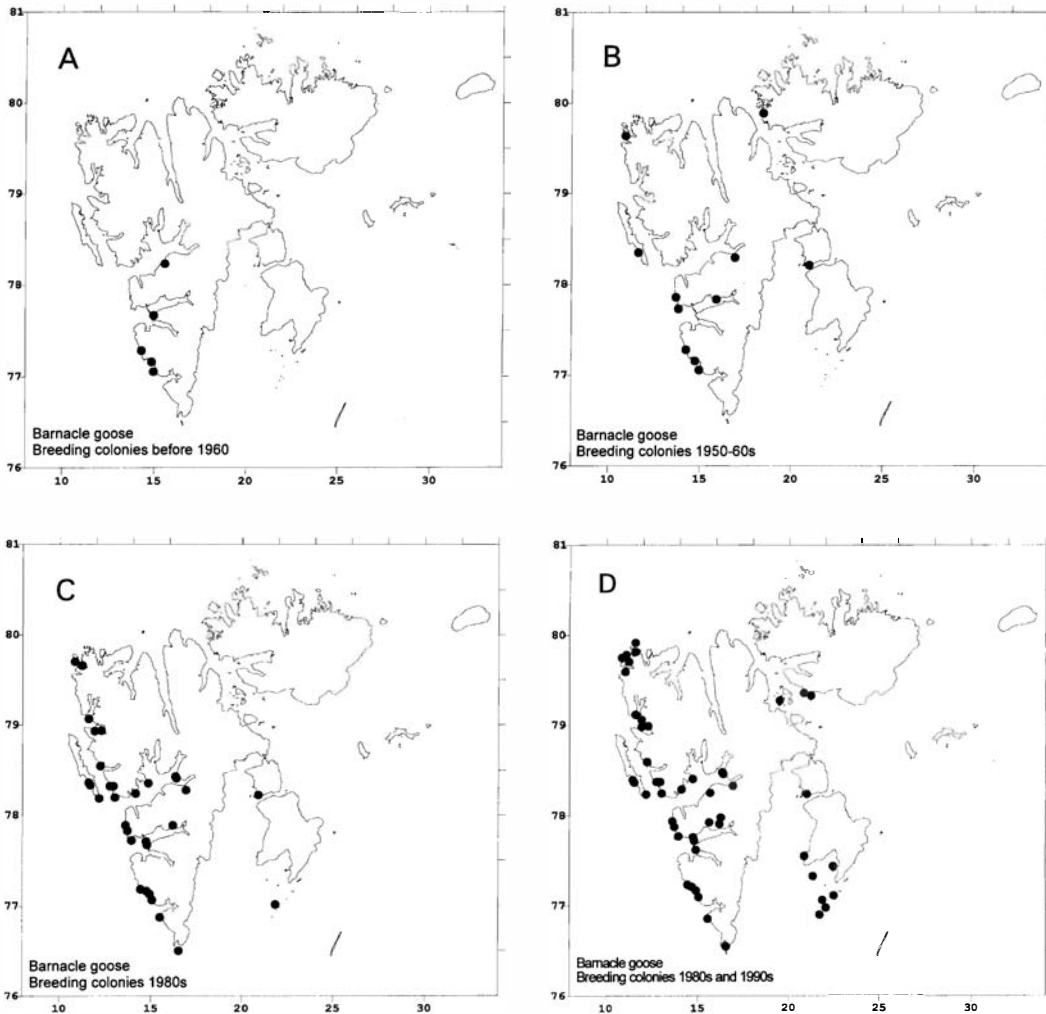


Fig. 3. Changes in the breeding distribution in Svalbard of barnacle geese *Branta leucopsis* from before 1960 to present: A. Before 1960 (Løvenskiold 1964); B. 1950–60s (Norderhaug 1970); C. 1980s (Prestrud et al. 1989); D. 1980s and 1990s.

breeding numbers at Dunøyane and Isøyane be might underestimated because polar bears *Ursus maritimus* had plundered the nests for eggs and only abandoned nest sites were recorded. Taking into account uncertainties in the counts, it is evident that some colonies have increased, whereas others are fluctuating but show no significant increasing or decreasing trends. The colonies with an increasing trend were all relatively newly established, and all but one of these (Bohemanneset) held less than 15 nests in the early 1980s.

Pink-footed goose

Prior to 1960 pink-footed geese were known to breed in coastal regions all along the western half of Spitsbergen (Fig. 4A). Additionally, a single record was known from Tusenøyane. The NP database contains relatively few nest records of pink-footed geese. Therefore, in presenting the breeding distribution in the period 1962–1996, all records of pink-footed geese observed in the breeding period (from 16 June to 31 July) have been used (Fig. 4B). This map shows no general

Table 1. Breeding pairs of barnacle geese *Branta leucopsis* in bird sanctuaries in Svalbard 1982–1996. Sanctuary Nos. refer to Fig. 1. Shading indicates colonies which give evidence of an increasing trend.

No	Sanctuary	1982 ¹	1983 ¹	1984	1986	1987	1990	1992	1993	1995	1996
1	Sørkapp	0									3
2	Dunøyane										
	Store Dunøya	240–350	210–300	400	250–320			428		216	
	Nordre Dunøya	150–180		180	220–300			192		194	
	Fjørholmen	145–175		100	80–100			99		54	
3	Isøyane										
	Nordre Isøya	85–105						419		202	
	Isøykalven	50–55						27		14	
4	Olsholmen	65–70			80–100			15		14	
6	Gåsøyane	3	6–8			35		130			385
7	Bohemanneset		45–65					109			
8	Plankeholmane	5–10						2			
9	Forlandsøyane										
	Sørøya	3	12–15	13	10–15			7		2	
	Midøya	260–300	200–280	450	300–400			226		353	
	Nordøya	100–110	70–110	115	70–90			73		64	
10	Hermansenøya		10–15					103			
11	Kongsfjorden	1	9	10		50	43	120*	291	247	240
12	Blomstrandhamna	0	0	1		0			32	29	39
13	Kapp Guisnez			7							16
14	Skorpa	15–25					12		10	1?	
15	Moseøya	100–125		170			139		176	25–30	

*Incomplete census.

¹From Prestrud & Børset (1984).

change in the distribution pattern, even though the number of observations is much larger. The species apparently is still rare in the eastern parts of Svalbard.

Distribution of pre-breeding flocks

Brent goose

Observations of brent geese in the pre-breeding period are mainly confined to the western coast of Spitsbergen and the two southern islands Bjørnøya and Hopen (Fig. 5A). Birds may arrive early at the nesting localities. I observed 24 individuals on the major nesting island Lurøya in Tusenøyane on 2 June 1986. At that time more than half of the island was snow-free. Pre-breeding flocks of brent geese have also been recorded at André tangen near the breeding colonies at Tusenøyane. The largest flock recorded in Svalbard during the pre-

breeding period was seen on the southwestern slope of Ingeborgfjellet near Vårsolbukta, Bell-sund on 6 June 1997 when ca. 200 birds were seen (J.O. Scheie pers. comm.). Brent geese also used this location on 31 May in the same year, when 60–70 birds were observed (B. Frantzen pers. comm.). An old record from 1930 (Kristoffren 1931) states that brent geese were seen at Sørkapp during spring migration, all arriving from east-south-east. Most individuals did not stay in the area but continued their migration along the western coast of Spitsbergen.

Barnacle goose

Records of barnacle geese in the pre-breeding period are remarkably few (Fig. 5B). Birds have been observed at Bjørnøya on several occasions, indicating that the island is a regular staging area for at least some barnacle geese. The maximum number of geese observed is about 600 indivi-

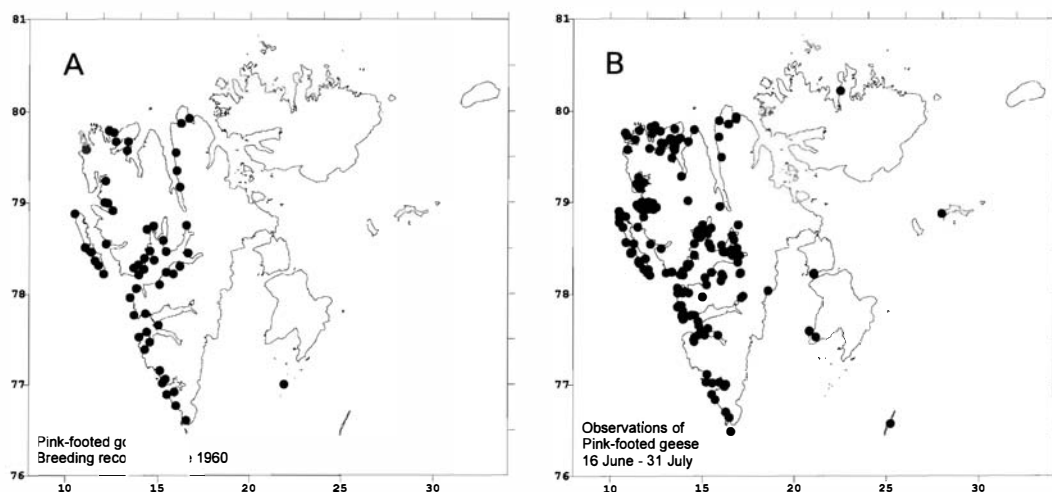


Fig. 4. A. Breeding distribution of pink-footed geese *Anser brachyrhynchus* in Svalbard prior to 1960 (after Løvenskiold 1964). B. Observations of pink-footed geese during the breeding period in the years 1962–1996. Norsk Polarinstitutt database.

duals in the period 17–24 May 1977 (Larsen 1978). Another apparently regular staging site comprise the vegetated slopes on the southwestern side of Ingeborgfjellet, near Vårsolbukta, Bellsund, where about 2000 geese (mostly barnacle geese) were seen on 31 May 1997, in snow-free parts of the tundra (B. Frantzen pers. comm.). Barnacle goose flocks have also been seen staging in hill slopes with little snow cover in Adventdalen. Other observations are from Brøggerhalvøya near the nesting localities in the Kongsfjorden area. There are also records from three localities in southeastern Svalbard.

Pink-footed goose

Records of pink-footed geese during the pre-breeding period include most of the locations where barnacle geese have been observed in the pre-breeding period (Fig. 5C). In addition to the southern islands Bjørnøya and Hopen and coastal areas on the western coast of Spitsbergen, the valleys in central Spitsbergen such as Adventdalen and Gipsdalen also seem to be important pre-breeding areas. A study from Gipsdalen (Frafjord 1990, 1993) showed that south-facing slopes in the outer part of the valley were used as foraging sites in late May, while north-facing slopes and

the flats at the bottom of the valley were used later when they were free of snow in early June.

Distribution of moulting and post-breeding flocks

Brent goose

Observations of brent geese in the period August–September cover almost all regions of Svalbard (Fig. 6A). The largest concentrations have been encountered at Tusenøyane and in the northern part of Spitsbergen from Moffen in the north to Liefdefjorden, Woodfjorden and Wijdefjorden in the south. During a helicopter survey on 15 Aug. 1989 along the shores in this region, a total of 353 individuals were observed (Fig. 7A). In a similar survey on 28–29 Aug. 1990, 85 brent geese were observed in the Liefdefjorden–Woodfjorden area (Fig. 7B), but no data were available from Moffen that year.

In Nordaustlandet most flocks observed have been small (<50 indiv.), but larger flocks have been encountered in Rijpfjorden and Augustabukta (Fig. 6A). Other areas where brent geese have been encountered include the coastal zone from Muchinsonfjorden to Lady Franklinfjorden (Fig. 6A). Dunøyane and Sørkapp are probably im-

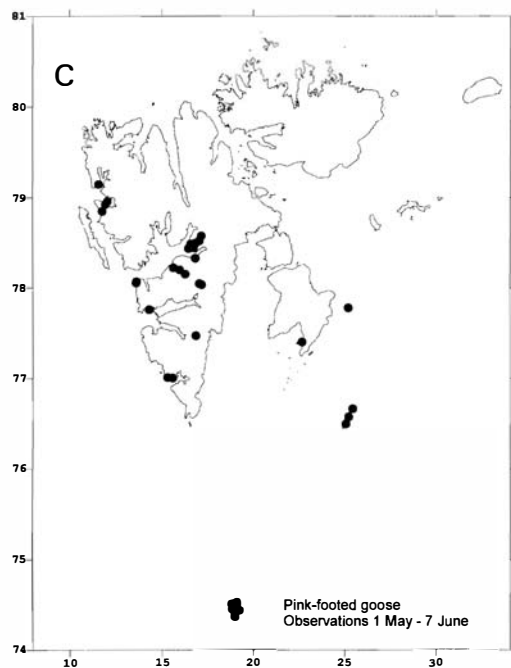
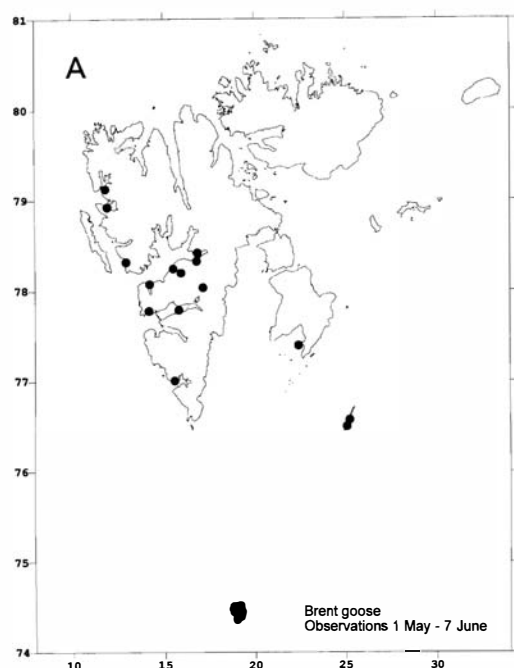
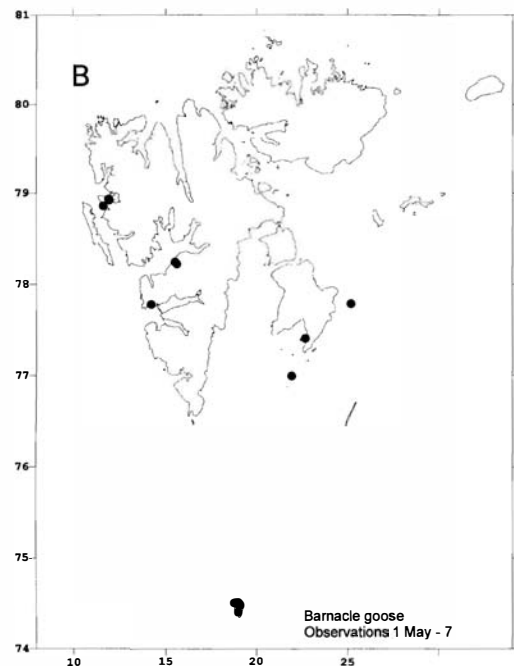
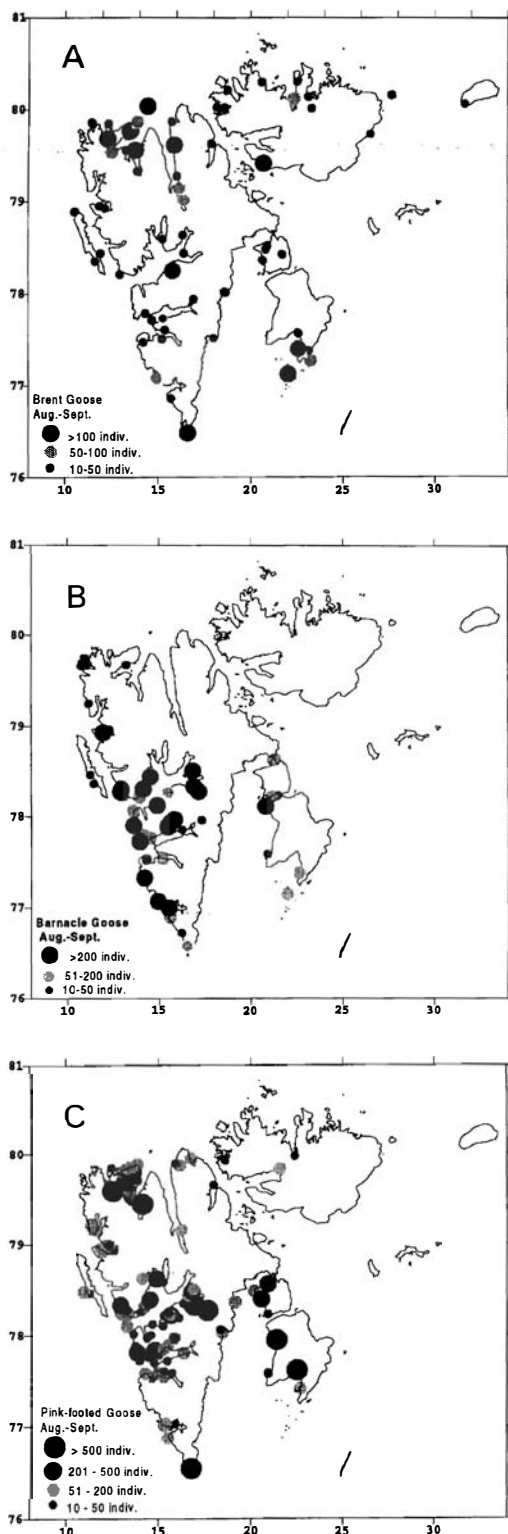


Fig. 5. Observations of brent geese *Branta bernicla hrota* (A), barnacle geese *Branta leucopsis* (B) and pink-footed geese *Anser brachyrhynchus* (C) in Svalbard during the pre-breeding period (1 May–7 June).



portant staging areas before the autumn migration (Fig. 6A). Kristoffersen (1931) stated that large flocks were seen along the coast at Sørkapp in the second half of August 1930, and that some of these birds came from breeding sites on the islands off Sørkapp. A flock of 120 individuals was seen at this location on 31 August 1964 (Heintz & Norderhaug 1966). Bjørnøya might be an important staging area during the autumn migration, and up to 350 individuals were observed on the island in the period 7–18 September 1984 (M. Owen pers. comm.). However, small flocks observed on the island in September of 1983 and 1984 probably stopped for less than an hour and did not feed much, if at all (J. Black pers. comm.).

Helicopter surveys in Storfjorden in 1989 and 1992 revealed that in addition to Tusenøyane, Tjuvfjorden, the western coasts of Barentsøya and Agardhbukta were also used as habitat for brent geese, albeit in lower numbers (Fig. 8).



Barnacle goose

Most of the important habitats for barnacle geese in August and September are located in coastal tundra from Isfjorden to Sørkapp. Other important areas include coastal tundra in the Kongsfjorden area as well as the coasts of Barentsøya and Edgeøya, and island habitats in Tusenøyane (Figs. 6B and 8).

The following areas have been recorded as holding ≥ 200 barnacle geese: Kongsfjorden, Daudmannsøya, Erdmannflya, Bohemanflya, Collesdalen, Gipsdalen, Sassendalen, Nordenskiöld kysten, Kapp Martin-Vårsoibukta, Reindalen, Elveflya-Storvika, Dunøyane, Hyttevika-Revelva, Hornsund North, and Kapp Lee. In some of these areas information is available on habitat use by barnacle geese.

Kongsfjorden: In Kongsfjorden most of the barnacle geese nest on small islands, but the families leave for the mainland just after hatching. The main chick-rearing and moulting area for barnacle geese breeding in Kongsfjorden is located within and just outside the human settlement of Ny-Ålesund. Loonen and collaborators (Loonen 1997; Stahl & Loonen 1998, this volume) have studied the habitat use of geese in Ny-Ålesund, and their main finding is that the presence of the arctic fox has a high influence on habitat use. In years without foxes in the area, the barnacle geese use a larger area around the settlement for foraging; when foxes are present, the geese aggregate in 'safe' areas near the lakes in the area. In addition to areas near Ny-Ålesund, some geese also forage on the tundra vegetation in other parts along the northern shores of Brøggerhalvøya as well as on Blomstrand(halv)øya on the northern side of Kongfjorden.

Daudmannsøya: Owen (1987) reported that in 1986 the barnacle geese families (360 adults and 107 juveniles) were largely concentrated near the lakes at the southwestern end of the area and on the inland lakes to the north.

Erdmannflya, Bohemanflya: Mitchell (1990) observed 620 barnacle geese in Erdmannflya and Bohemanflya in 1990. The birds were seen in flocks scattered over most of Erdmannflya and the

Fig. 6. Observations of flocks of brent geese *Branta bernicla hrota* (A), barnacle geese *Branta leucopsis* (B), and pink-footed geese *Anser brachyrhynchus* (C) in Svalbard during post-breeding (August and September).

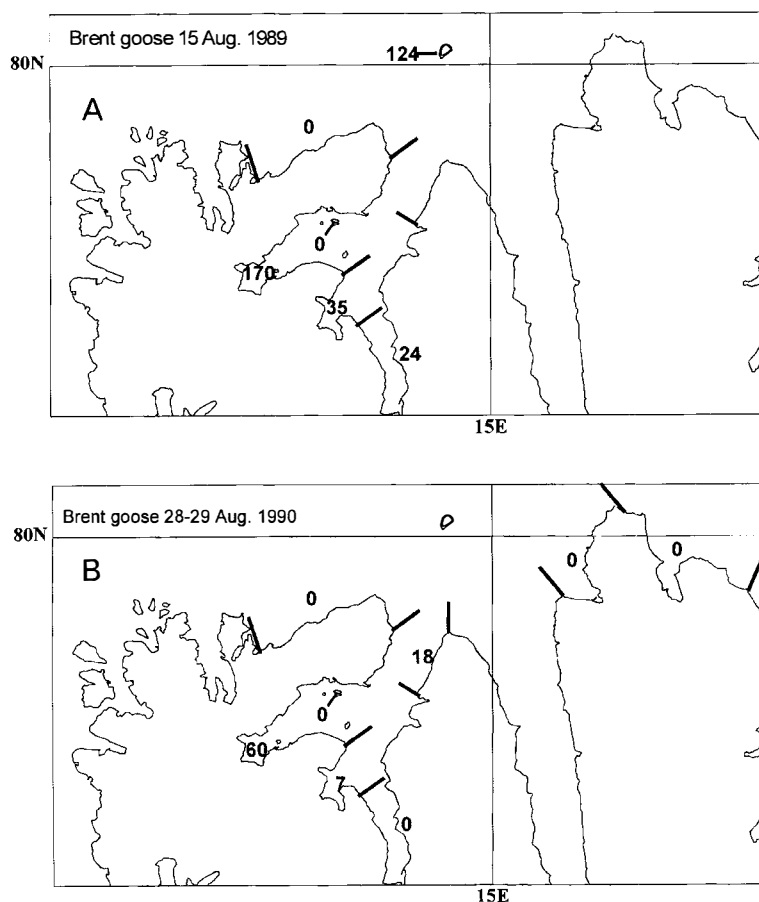


Fig. 7. Results of helicopter censuses of brent geese *Branta bernicla hrota* on 15 August 1989 (A) and 28–29 August 1990 (B) in northern Spitsbergen. Numbers refer to individuals observed.

eastern parts of Bohemanflya, areas characterised by small lakes.

Colesdalen: The vegetated areas around lake Tenndammen near Colesbukta are probably the most important habitat for barnacle geese. In 1995 a total of 325 and 312 individuals were observed on 18 July and 7 August, respectively (Bangjord 1997).

Gipsdalen: During a survey in 1990 (Mehlum 1990), barnacle geese were only found in vegetation types classified by Elven et al. (1990) as wet moss tundra and swamps. The birds were seen at two small lakes and in two wet tundra areas. Delany & Choudhury (1994) observed a total of 281 barnacle geese in similar vegetation types in Gipsdalen in 1994.

Sassendalen: Patterson et al. (1995) caught moulting barnacle geese for ringing purposes near the mouth of Sassendalen in 1995. Two flocks

comprising 60 and 30 individuals were associated with two lakes on either side of the river Sassenelva ca. 2.5 km from the coast.

Nordenskiöldkysten: Detailed investigations on habitat use by barnacle geese during the moulting and the growth periods of the goslings are available from Nordenskiöld kysten (Owen et al. 1978; Drent et al. 1998, this volume; R.H. Drent pers. comm.). Drent (pers. comm.) names 53 sites in this region which are frequented by the geese (Fig. 9). These are all associated with fresh water.

Reindalen: The first records of barnacle geese from the area around the lakes Stormyrvatna in lower Reindalen date back to 1954 when 23 adult birds were captured and ringed (Goodhart et al. 1955). This area and areas around the mouth of Reindalselva have since been regular habitats for barnacle geese. In 1989, a minimum of 700 individuals (only one family with goslings) were

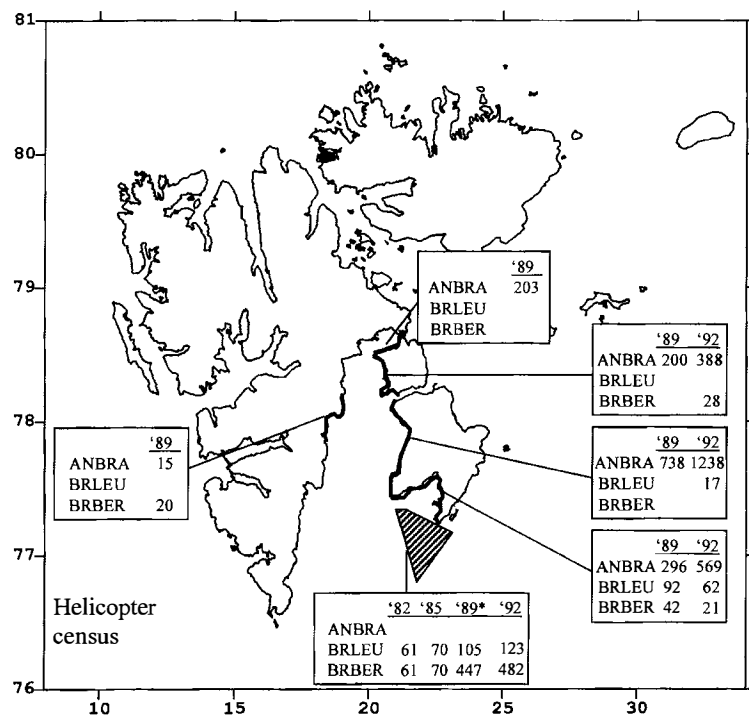


Fig. 8. Results of helicopter censuses of moulting geese in southeastern Svalbard (ANBRA: pink-footed geese *Anser brachyrhynchus*; BRLEU: barnacle geese *Branta leucopsis*; BRBER: brent geese *Branta bernicla hrota*). Numbers refer to individuals observed. The censuses were conducted in 1982, 1985, 1989 and 1992.

observed in the period 27 July–2 August (NP). In 1994 a total of ca. 1000 barnacle geese were present in the lower part of Reindalen by the end of July–early August (Jacobsen & Tyler 1994).

Pink-footed goose

During August and September large concentrations of pink-footed geese have been recorded along most of the western and northern coasts of Spitsbergen, as well as on the western coasts of Barentsøya and Edgeøya. Flocks larger than 500 individuals have been observed in Liefdefjorden–Woodfjorden, Adventdalen–Sassendalen, Sørkapp in Spitsbergen, and in Diskobukta and Tjuvfjorden in Edgeøya (Fig. 6C). On helicopter surveys along the western coasts of Barentsøya and Edgeøya (Fig. 8), a total of 1,437 individuals were observed on 10–11 August 1989, and 2,195 on 21 and 26 July 1992. A total of 2,167 pink-footed geese were observed on a helicopter survey along the coasts of Liefdefjorden–Woodfjorden on 15 August 1989 (Fig. 10A), whereas only 317 were seen in the same area on 29 August 1990 (Fig. 10B).

As for the other Svalbard goose species, Bjørnøya is an important staging area for at least parts of the population. Owen (pers. comm.) observed max. daily numbers of 1,000–2,000 pink-footed geese staging on the island in early October 1984.

Discussion

The largest change from the 1950s to the present in breeding distribution among the three species of geese breeding in Svalbard has been documented for the barnacle goose. The expansion in breeding distribution coincides with the increase in the population size from about 300 birds in the late 1940s to the present level of 23,000 individuals (Madsen et al. 1998, this volume). It seems that as the population increased, the relatively densely populated bird sanctuaries reached their carrying capacity (Table 1), and further increase in the breeding population was facilitated by the establishment of new colonies. These new colonies are located within the former breeding range along the western coast of

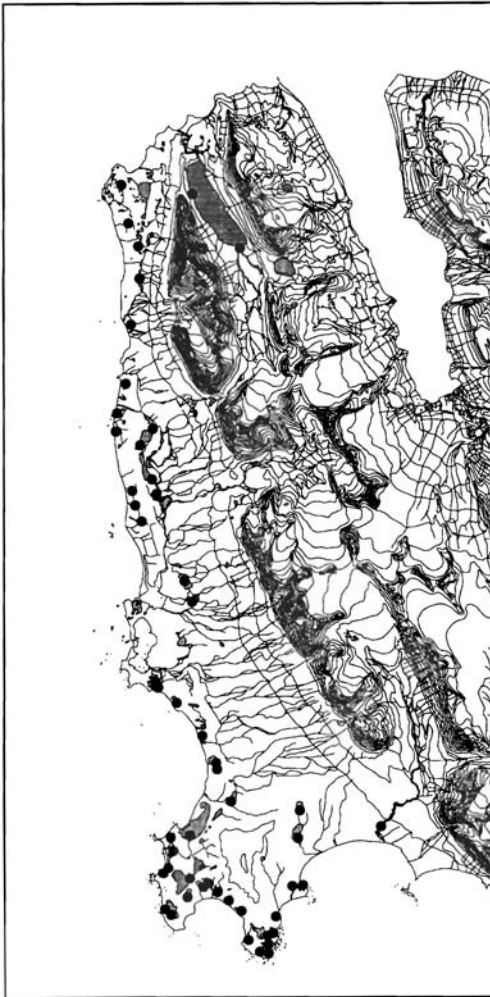


Fig. 9. Fresh-water ponds and lakes along Nordenskiöldkysten, western Spitsbergen, frequently used by moulting and gosling-rearing barnacle geese *Branta leucopsis* (Data from R.H. Drent, pers. comm.).

Spitsbergen, as well as in new areas further north and east in the Svalbard archipelago.

Knowledge of the current breeding distribution of brent geese in Svalbard is incomplete. However, it is almost certain that the main breeding area is Tusenøyane, where brent geese have been recorded breeding on most islands (Persen 1986; Madsen et al. 1989; Bregnballe & Madsen 1990; Bustnes et al. 1995). The island Moffen is also an important breeding locality. From the abundance of brent geese seen on our August aerial surveys,

we suspect that more breeding localities may be located in the northern parts of Spitsbergen.

It is also suspected that more breeding localities exist in the fjords on the northern and western parts of Nordaustlandet. Due to logistical problems (late breakup of sea-ice), most recent visits made by ornithologists to these regions are from the post-breeding period. Flocks of brent geese have frequently been recorded, but breeding has rarely been confirmed. The studies initiated in 1997 (Clausen & Bustnes 1998, this volume) applying satellite telemetry may reveal a better knowledge of the breeding localities of brent geese in Svalbard.

The pink-footed goose has a widespread breeding distribution in Svalbard, but no systematic effort have been made to map its breeding localities. However, it is assumed that the data presented in Fig. 4 of records of pink-footed geese observed during the summer fairly well reflects the breeding distribution. This species breeds in single pairs or loose colonies in coastal regions and on islands. The population has experienced an increase in numbers similar to the barnacle goose during the last decades (Madsen et al. 1998, this volume), but according to the data available this has not caused a significant geographical expansion of the breeding distribution in the Svalbard archipelago.

Owen & Norderhaug (1977) pointed out that barnacle geese have occupied the islands where brent geese previously bred, and that a further expansion of the barnacle goose population may be to the detriment of the brent goose because of the competition for nest sites or food. Thus, in the bird sanctuaries, where the number of breeding barnacle geese has reached the carrying capacity, the brent goose may not be able to increase in numbers. Madsen et al. (1989) observed that aggression between the two species was regular on Tusenøyane, where they co-occur as breeders. Prospecting barnacle geese pairs were mostly expelled from brent goose territories, even though brent geese are smaller. Owen & Norderhaug (1977) suggested that barnacle geese nest earlier than brent geese and thus have a competitive advantage in occupying nest sites. At Tusenøyane, however, the barnacle geese started egg-laying three weeks later than brent geese in 1987 (Madsen et al. 1989). It is still unclear to what extent competition for nest sites and food resources limits the growth of the brent goose population in Svalbard.

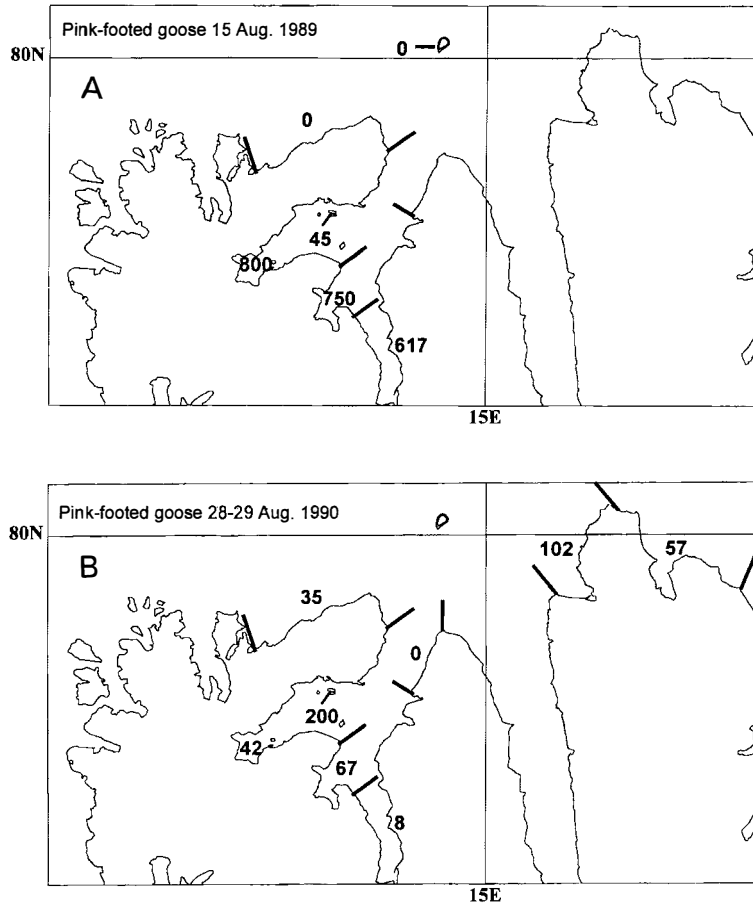


Fig. 10. Results of helicopter censuses of pink-footed geese *Anser brachyrhynchus* on 15 August 1989 (A) and 28-29 August 1990 (B) in northern Spitsbergen. Numbers refer to individuals observed.

The potential for competition for nest sites between barnacle geese and common eiders has also been a subject of discussion (Prestrud & Børset 1984; Prestrud & Mehlum 1991). Most of the islands where barnacle geese have increased in numbers are occupied by eiders. Studies in Kongsfjorden indicate that the increase in the number of the barnacle goose nests on an island does not have a negative impact on the number of eider nests (Tombre et al. 1998, this volume). In the study of the inter-annual variation in the number of nests on selected islands in Kongsfjorden, a positive relationship between the numbers of nests of eiders and barnacle geese was obtained.

Tombre et al. (1996) have shown that barnacle geese use on average three weeks from their departure from the spring-staging areas in Helgeland, Norway, to their arrival at the nesting islands

in Kongsfjorden. Tombre et al. (1996) thus argue that the geese must spend a considerable amount of time elsewhere. They also showed that late arriving geese had more body reserves than those which arrive early at the breeding places. This supports the hypothesis that the geese are able to forage during the migration between the spring-staging areas in Helgeland and the breeding places in Svalbard.

The availability of snow-free ground probably is a determinant factor for the location of pre-breeding staging areas for the three goose species breeding in Svalbard. Although the knowledge of the locations of such areas is still incomplete, some localities have been identified as areas frequently used by the geese. South-facing slopes in the coastal regions of western Spitsbergen seem to be important pre-breeding staging areas. Among these are the slopes below Ingeborgfjellet

in Bellsund and the slopes in Gipsdalen and Adventdalen in Isfjorden.

Some geese may fly more or less directly to their breeding localities, such as brent geese in Tusenøyane, where the geese have been observed as early as 2 June. This is shortly after the normal peak migration period recorded on the coast of southern Norway, which is 26–31 May (Clausen et al. 1999). Further studies with the use of satellite telemetry would be useful for obtaining more information of the use of pre-breeding staging areas for the three goose species in Svalbard.

Post-breeding concentrations of geese have been found over most of the coastal regions of the archipelago. Barnacle geese breeding on islands usually leave their nest localities and move to coastal tundra areas characterised by small lakes surrounded by lush vegetation. Although the extent to which geese fly from their moulting areas near their breeding sites to other pre-migration staging areas in Svalbard is not known, there are indications that at least part of the geese populations fly to specific pre-migratory staging sites. Studies of barnacle geese equipped with satellite transmitters have shown that they spent about three weeks near the southern coasts of Isfjorden after departure from their breeding sites in Kongsfjorden and before leaving for Bjørnøya (Butler & Woakes 1998, this volume).

This finding is in accordance with sightings of large flocks of barnacle geese in this region in August–September.

Old records show that the northern shores of the Isfjorden area may have been, at least in previous times, a staging area for brent geese in the autumn. Torell & Nordenskiöld (1869) observed thousands of brent geese at Kapp Thorsden on 1 September 1861, and Van Oordt (1921) observed more than a thousand individuals in late August in the Ekmanfjorden area.

Another staging area is the shores of Hornsund. Kristoffersen (1926) described a staging area in the vicinity of Camp Erna on the southern side of the mouth of Hornsund. Here large numbers of pink-footed geese gathered in September, and from two to three thousand individuals had left the area by the end of the month.

Aerial transects revealed large numbers of brent and pink-footed geese along the shores of northern Spitsbergen in August. The number of both species of geese observed was lower on 28–29 August 1990 than on 15 August 1989. These

results, even if not conclusive, may indicate that many of the geese move out of this area during the second half of August.

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The Kongsfjorden colony of barnacle geese: Nest distribution and the use of breeding islands 1980–1997

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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 Polarinstitutt Skrifter* 200.

The Kongsfjorden colony of barnacle geese in Svalbard was established in the early 1980s. This paper presents a fifteen-year data set of nest distribution and individual use of different nest locations are presented for the geese breeding in this colony. Nest site fidelity, clutch sizes and a relation between numbers of goose nests and common eider nests are also investigated. The first nest of barnacle geese were observed in Kongsfjorden in 1980. Numbers have since increased on all nest locations (mainly islands). In 1997, 329 barnacle goose nests were recorded in Kongsfjorden, the largest concentrations of nests being found on Storholmen and on Juttaholmen. Two-thirds of the females had a high fidelity to their breeding island, whereas the rest showed a medium low fidelity to their nest site. Poor breeding conditions, a combination of sea ice around breeding islands and egg predation by arctic foxes were probably the main reasons for shifts in nest sites. Average clutch sizes were similar in most years and on most islands, although some variation has occurred within some islands (no directional trend). No relationship between clutch size and nest number on the different islands was found. A positive relationship between the number of goose nests and the number of common eider nests was found on four islands, which reflects the importance of sea-ice conditions and island availability for successful nesting. No increase in the percentage of goose nests relative to common eiders nests was recorded during the last five years. This indicates that no obvious competition for nest sites has existed between the two species. Even if sea ice conditions and the presence of foxes proximately influence breeding conditions on the different islands, nest site *per se* is presumably not the determining factor for clutch size and breeding success.

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Introduction

The population of barnacle geese *Branta leucopsis* breeding in Svalbard has increased considerably since the 1940s (Owen 1984; Black 1998, this volume). The current population estimate is approximately 23,000 geese (Madsen et al. 1998, this volume). The population winters in a restricted area in the Solway Firth in southwest Scotland and northwest England, but on the breeding grounds in Svalbard the geese breed in many colonies scattered mainly in the western parts of the archipelago (Mehlum 1998, this volume). The colonies in Svalbard have been established successively, giving significant differences in the age of the colonies (Prestrud et al. 1989; Black 1998, this volume). Originally, the barnacle geese in Svalbard nested on cliff faces and rocky slopes (Løvenskiöld 1964), but at present most colonies

are located on offshore islands and on a few inland cliffs (Prestrud et al. 1989; Mehlum 1998, this volume). Barnacle geese feed during the incubation period, and distance to food from the nest site may be an important parameter in nest site selection (Prop et al. 1984). The colony in Kongsfjorden in the vicinity of the Ny-Ålesund village (78°55'N, 12°00'E) was established in the early 1980s and consists today of almost 800 individuals (Loonen et al. 1998, this volume). The majority of the geese breed on islands in Kongsfjorden, but some geese also breed on the mainland near Ny-Ålesund village and on an adjacent bird cliff (Mehlum unpubl.; Tombre 1995; Loonen 1997).

This paper presents data on nest distribution and individual use of different nest locations in the Kongsfjorden colony of barnacle geese in Svalbard. The colonisation of the different islands from 1980, when the first nest was found, to the present, when more than 300 nests are distributed on

several islands, is described. Nest site fidelity for individual females in the period 1992–1997 is examined, and differences in clutch sizes between islands and possible changes in clutch sizes over years within each island are evaluated. During 1993–1997, the total number of breeding geese has been relatively stable (Loonen 1997), though the numbers of breeders have varied among islands. The islands are also important breeding islands for common eiders *Somateria mollissima*, and in order to reveal a possible competition for nest sites between the two species, we compared the number of barnacle geese and common eider nests on islands where the number of goose nests have varied more than 50%.

Study area and methods

The study area, Kongsfjorden with the islands and the Ny-Ålesund village, is shown in Fig. 1. Islands without names on the map are islands rarely used by geese (or by common eiders) because the general late break-up of fjord ice around these islands exposes them to egg predation by arctic foxes *Alopex lagopus* breeding in the inner part of the fjord (Mehlum 1991a). The islands were censused each year from 1981 to 1997, except in

1986 and 1988. In 1989, 1990 and 1992 censuses are available from only some nest locations. Nest locations censused were Prins Heinrichøya (3 ha), Dietrichholmen (0.15 ha), Miehtholmen (0.4 ha), Storholmen (30 ha), Juttaholmen (2 ha), Eskjer (1 ha), Ytre Breøya (3 ha) and the Ny-Ålesund village with adjacent areas (300+ ha) (Fig. 1). After hatching, families bring their young from the islands to the Ny-Ålesund area, which is the major brood rearing site (Loonen 1997). For further description of the colony and the study area see Tombre (1995) and Loonen (1997).

All islands were visited by boat and searched systematically for nests. Nests were counted once during the incubation period (last week of June–first week of July). In some years we also recorded the date when the fjord ice broke up around the different islands.

More than 70% of the adults in the Kongsfjorden colony are now individually marked with coded plastic leg bands and metal rings. The plastic rings can be read through telescope from more than 200 m (for details of the ringing procedures see Owen & Black 1989; Black & Owen 1995; Loonen et al. 1998, this volume).

In the period 1992–1997, rings were intensively recorded on nest locations in order to evaluate nest site fidelity between years for individual females. Only females which were seen in at least three different seasons or more were used in the analyses (females seen less than three seasons, $n = 252$, females seen more than three seasons, $n = 166$). Every year some females were observed with goslings later in the season but their nest sites were unknown. Females seen in three seasons with unknown nest site in two of the seasons were deleted from the nest site fidelity analyses. This was also true for females seen in four seasons with unknown nest sites in two or more seasons, for females seen in five seasons with unknown nest site in three or more seasons and for females seen in six seasons with unknown nest sites in three or more seasons. We allowed some unknown nest sites in the remaining sample ($n = 112$) and defined an unknown nest site as a 'new' nest site. An unknown nest site could therefore also have been the same nest site as in the previous year. Nest site fidelity was defined at three different levels: high, medium and low (Table 1).

With the exception of Dietrichholmen and Ny-Ålesund, clutch sizes were recorded on all nest locations in 1991–1993 and in 1995–1997. Clutches with one egg were assumed to be in-

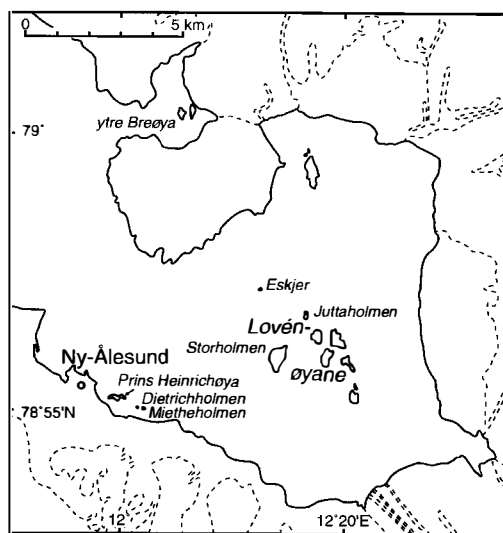


Fig. 1. Location of Ny-Ålesund and the islands in Kongsfjorden, Svalbard. Islands without names are rarely used by the barnacle geese.

Table 1. Definitions of nest site fidelity for barnacle geese breeding in Kongsfjorden, Svalbard.

Level of nest site fidelity	Percentage of fidelity (number of seasons nesting at the same site)
High	83% (5 of 6 seasons)
	80% (4 of 5 seasons)
	75% (3 of 4 seasons)
	67% (2 of 3 seasons and 4 of 6 seasons)
	60% (3 of 5 seasons)
Medium	50% (2 of 4 seasons and 3 of 6 seasons)
	40% (2 of 5 seasons)
Low	33% (1 of 3 seasons and 2 of 6 seasons)
	25% (1 of 4 seasons)
	20% (1 of 5 seasons)
	17% (1 of 6 seasons)

complete clutches and deleted from the analyses. Common eider nests were counted on Mietheholmen, Prins Heinrichøya, Storholmen and Juttaholmen in 1993 and in 1995–1997.

Results and discussion

Number of nests

Since the first nest in the Kongsfjorden area was found in 1980, there has been a general increase in nest numbers at all locations, except at Ny-Ålesund (Fig. 2, linear regressions, Ny-Ålesund: $R^2 = 0.08$, $n = 14$, $p = 0.31$, Prins Heinrichøya: $R^2 = 0.33$, $n = 13$, $p = 0.03$, Dietrichholmen: $R^2 = 0.52$, $n = 11$, $p = 0.01$, Mietheholmen: $R^2 = 0.30$, $n = 13$, $p = 0.05$, Storholmen: $R^2 = 0.50$, $n = 14$, $p = 0.001$, Juttaholmen: $R^2 = 0.61$, $n = 12$, $p = 0.003$, Eskjer: $R^2 = 0.71$, $n = 12$, $p = 0.001$, Ytre Breøya: $R^2 = 0.75$, $n = 12$, $p = 0.0003$). The first nest locations colonised were Ny-Ålesund and Dietrichholmen, and from 1983 nests were also found on Prins Heinrichøya, Mietheholmen and Juttaholmen. Today, the largest concentration of geese is on Storholmen (41.3% of the nests in 1997), although in recent years Juttaholmen has also become important (21.6% in 1997, Fig. 2).

Due to exposure to fox predation, the number of

nests on each island is influenced every year by the general sea-ice conditions as well as the location of the nests in relation to the extent of sea ice. Regardless of the ice conditions in the fjord, the number of nests in the Ny-Ålesund village will depend on the presence of foxes. On the basis of their geographical position, nest locations were grouped in four categories: (1) Ny-Ålesund, (2) the Ny-Ålesund islands (Prins Heinrichøya, Dietrichholmen, Mietheholmen), (3) Lovénøyanne (the inner-fjord islands Storholmen, Juttaholmen, Eskjer) and (4) Ytre Breøya (Fig. 1).

Ny-Ålesund

In general, since the first nest was found at Ny-Ålesund in 1980, the village has hosted few barnacle goose nests (Fig. 2). In 1987, 1990 and 1991, no foxes were seen at Ny-Ålesund and a few geese nested successfully (1987: $n = 10$, 1990: $n = 10$, 1991: $n = 22$). Some preferred nest sites disappeared in 1992 when a new dock was built at Ny-Ålesund. Seven nests were found in 1992, but because several foxes visited the village that year, nesting success was low for the geese attempting to breed there. There were foxes at Ny-Ålesund in the following years as well (1993–1995), but despite the foxes, a few nests located on rocks were successful. In 1996 and 1997, no foxes were observed in the village and a few successful nests were found on the tundra near the village.

At Ny-Ålesund, and nearby, there are plenty of potential nesting sites for barnacle geese. The area is also extensively used for feeding in the brood rearing period (Loonen 1997). Restrictions in space and food availability during nesting are presumably not the limiting factor for nest numbers at this location, fox predation being more likely to determine nest numbers at Ny-Ålesund. Predation by foxes is also thought to be the main reason why barnacle geese are basically cliff or island nesters (Norderhaug 1970; Mehlum & Ogilvie 1984). In years with late break-up of sea ice, however, Ny-Ålesund may be the best alternative for nesting because geese nesting on the islands suffer relatively more from fox predation, as is the case with common eiders (Mehlum 1991b).

The Ny-Ålesund islands

The Ny-Ålesund islands are located close to the

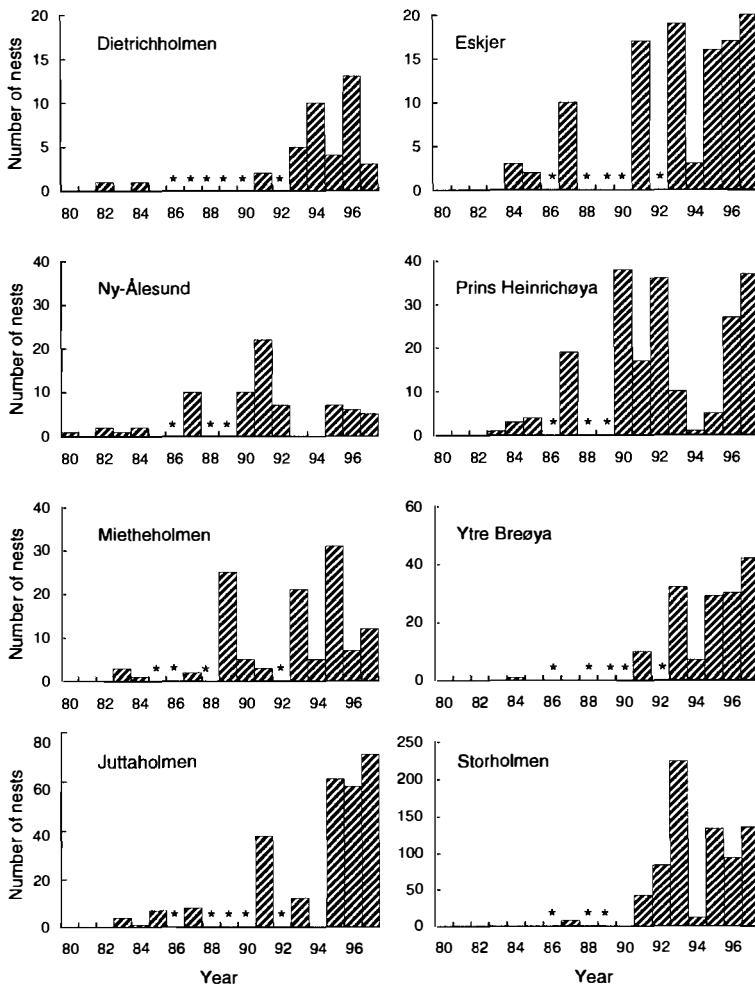


Fig. 2. Barnacle goose nests in breeding locations in the Kongsfjorden area, 1980–1997. Stars indicate years without nest recordings. Note the different scales on the y-axes. Since 1980, there has been a general increase in nest numbers, except in the Ny-Ålesund village where numbers have been low since the first pairs were recorded.

mainland. Due to shallow water, Prins Heinrichøya in particular often has an ice-bridge connecting the island to the mainland. The timing of ice break-up does not necessarily occur at the same time for the different islands because ice conditions are influenced by differences in local factors such as sea depth and distance from the mainland (Table 2). After 1991, peak nest numbers occurred in years when the islands were ice-free before June (Table 2, Fig. 2), with a few exceptions. Dietrichholmen and Mithelholmen were ice-free in late May in both 1996 and 1997 but had fewer nests in those years (except Dietrichholmen in 1996). In both years, Prins Heinrichøya had ice conditions similar to those of the other two islands, and some geese may have shifted to this larger

island. For eiders, unfavourable sea ice conditions have been found to force the birds to nest at higher densities on small islands (Parker & Mehlum 1991). On Prins Heinrichøya, at least in the early season, the geese can feed on the island during the incubation period. On the small islands, the geese have no opportunities to feed during incubation, and the islands are also further away from the preferred feeding areas at Ny-Ålesund (Loonen 1997). Unfortunately, there are no data to confirm such a shift in nesting sites since ring readings from Dietrichholmen and Mithelholmen are limited in 1995 and 1996.

Based on the number of nests, the last successful years suggest an upper limit in carrying capacity of goose nests on these islands. In addition to geese,

Table 2. The dates when different islands were free of sea ice, 1992–1997. Note that there were no foxes in Kongsfjorden in 1996 and 1997.

Year	Date					
	Prins Heinrichøya	Mietheholmen	Dietrichholmen	Storholmen	Juttaholmen	Eskjer
1992	1 June (–) ¹⁾	* ²⁾	*	1 June (–)	*	*
1993	25 June	11 June	11 June	3 June	*	*
1994	23 June (+) ³⁾	14 June	10 June	25 June	20 June (+)	16 June
1995	18 June	1 June	1 June	15 June ⁴⁾	10 June	1 June
1996 ⁵⁾	31 May	28 May (–)	28 May (–)	16 May	15 May	28 May (–)
1997 ⁵⁾	2 June (–)	2 June (–)	2 June (–)	2 June	15 June	2 June (–)

¹⁾ (–) = ice gone before this date.

²⁾ * = lack of information.

³⁾ (+) = ice-bridge also after this date.

⁴⁾ The island was 'guarded' from early June to prevent egg-predation by foxes.

⁵⁾ No foxes in Kongsfjorden.

common eiders breed in dense concentrations on these islands (Mehlum 1991a). Common eiders may therefore influence the space available for nests (see below).

Lovénøyane

Due to their geographical position, the inner-fjord islands are more exposed to fox predation than the Ny-Ålesund islands in years with late break-up of fjord-ice (except Prins Heinrichøya, see earlier). In general, these islands are larger, and on Storholmen, the largest island, the geese usually feed on the island during the whole nesting period (Alsos 1995; Tombre & Erikstad 1996).

The total production of young in Kongsfjorden was high in 1991, resulting in many new nests in 1993 (29 first-time breeders on Storholmen) (Dalhaug et al. 1996; Loonen 1997). On Storholmen, 84 nests in 1992 increased to 224 nests in 1993. On Juttaholmen, however, only 12 nests were found in 1993, probably because a late break-up of sea ice (late June) for this island. In recent years, there has been an increase in the number of nests on Juttaholmen (Fig. 2). Females may therefore have moved from Storholmen to Juttaholmen since fewer geese nested on Storholmen in 1995–1997 than in 1993. Ten of 20 females (50%) with known rings breeding on Juttaholmen in 1996 have bred on Storholmen in earlier years (breeding at least once on Storholmen), and eight of 17 females (47.1%) on Juttaholmen in 1997 have bred on

Storholmen earlier. The shift in breeding island after 1993 could have been caused by the breeding conditions in 1994. In 1994, the fjord-ice surrounded Lovénøyane until late June and several foxes were harvesting eggs from the island. Only 11 nests on Storholmen (late breeders) hatched successfully (successful defined as at least one gosling leaving the nest) in 1994 (Fig. 2). The low success may therefore have caused some Storholmen breeders to move to Juttaholmen the following years instead (and vice versa). As research activity has been more frequent on Storholmen than on Juttaholmen in recent years, some geese may have preferred Juttaholmen over Storholmen because of human disturbance. However, as research activity has continued since 1992, we would have expected a shift earlier than in 1995 if disturbance was the main reason for the shift in nesting site. The extreme breeding conditions in 1994 probably caused some geese to change nest site, but whether or not human activity is the main cause of shift in nesting sites can only be determined by continued monitoring in future breeding seasons.

The 1993 count at Storholmen demonstrates that the island can support at least 224 barnacle goose nests (Fig. 2). The island has therefore been carrying less than its potential capacity of goose nests in 1994–1997.

Nest numbers have remained relatively stable on Eskjer since 1991, except the extreme season in 1994, and this island may have reached its maximum for potential goose nests. The island provides

little vegetation and is also relatively distant from alternative feeding areas. Because nest numbers have increased on Juttaholmen, it is difficult to predict the upper limit of goose nests there.

Ytre Breøya

Barnacle geese breeding on Ytre Breøya are somewhat isolated from the rest of the colony. In the brood rearing period at Ny-Ålesund, there are fewer sightings of families from Ytre Breøya than sightings of families from the other islands (Loonen unpubl.). Geese ringed during moult at Ny-Ålesund and recorded as breeders at Ytre Breøya have not been seen breeding on any other nest location in Kongsfjorden. Numbers have increased on this island, and currently there are no signs of nest numbers levelling off (Fig. 2).

Nest site fidelity

Almost two thirds of the females seen in at least three different seasons in Kongsfjorden (66.1%, $n = 74$) were classified as showing a high level of nest site fidelity. Only 6.3% ($n = 7$) of the females showed a low nest site fidelity, while 27.6% ($n = 31$) of the females had medium fidelity to their nest location. These results support the general high level of fidelity, both to nest sites and feeding areas, found for most waterfowl (Owen & Black 1990; Anderson et al. 1992; Cooke et al. 1995). For arctic-nesting geese, fidelity is suggested to be highly advantageous because the short breeding season favours familiarity to the breeding grounds (Owen & Black

1990). For common eiders, nest site fidelity on the breeding ground has been found to be positively correlated with nesting success (Bustnes & Erikstad 1993) and results from the present study suggest that this may be the case also for the barnacle geese in Kongsfjorden. The poor breeding season in 1994 was probably one of the main reasons why some females switched breeding island in 1995 and 1996. Even if almost 70% of the females nesting in Kongsfjorden showed a high nest site fidelity, it is obvious that females sometimes do change nest site within the colony if breeding conditions for some reasons become unfavourable. The philopatry on a larger scale is also high, and more than 85% of the females are known to return to Kongsfjorden every spring (Loonen et al. 1998, this volume; Tombre et al. 1998, this volume).

Clutch sizes

The variation in clutch sizes was small, both between years and between different nest sites (Table 3). The most frequent clutch size consisted of four eggs, with two exceptions. The most common clutch size on Storholmen in 1993 was three eggs and because young barnacle geese produce fewer eggs (Forslund & Larsson 1992), smaller clutches were probably due to the high proportion of first time breeders on this island in 1993. In 1995, the most common clutch size on Eskjer was three eggs, but the age of the breeding birds was unknown.

There were no significant differences between years in average clutch sizes on Eskjer, Prins

Table 3. The average clutch size (\pm SE) on six different islands for barnacle geese in Kongsfjorden, Svalbard. No complete clutches were found in 1994 due to extreme sea ice conditions and heavy egg-predation by arctic foxes. A comparison of clutch sizes among years (ANOVA) was made separately for Storholmen and Juttaholmen, two important nest locations. Similar letters indicate no significant differences between years. Sample sizes in parentheses, asterisks indicate missing data.

Year	Prins Heinrichøya	Mietheholmen	Storholmen	Juttaholmen	Eskjer	Ytre Breøya
1991	4.0 \pm 0.2 (17)	*	4.2 \pm 0.1 (41) A	3.9 \pm 0.1 (38) AB	4.3 \pm 0.3 (16)	3.6 \pm 0.3 (10)
1992	3.5 \pm 0.2 (30)	*	3.4 \pm 0.1 (73) C	*	*	*
1993	*	*	3.3 \pm 0.1 (194) C	*	*	*
1995	*	4.0 \pm 0.1 (30)	3.9 \pm 0.1 (94) B	4.1 \pm 0.1 (53) A	3.5 \pm 0.3 (13)	3.8 \pm 0.2 (28)
1996	3.8 \pm 0.2 (25)	*	4.0 \pm 0.1 (186) AB	3.5 \pm 0.1 (45) BC	*	3.8 \pm 0.1 (28)
1997	3.9 \pm 0.2 (37)	3.7 \pm 0.3 (12)	3.7 \pm 0.1 (113) B	3.4 \pm 0.1 (63) C	4.1 \pm 0.2 (19) 3	3.9 \pm 0.1 (32)

Heinrichøya or Ytre Brøya (ANOVA, Eskjer: $F = 2.63$, $df = 2, 45$, $p = 0.1$, Prins Heinrichøya: $F = 1.43$, $df = 4, 129$, $p = 0.2$, Ytre Brøya: $F = 0.37$, $df = 3, 94$, $p = 0.8$). On Juttaholmen and Storholmen, mean clutch sizes varied between years but there were no trends in either direction over the last seven years (Table 3). Average clutch sizes partly followed the dates when the sea ice broke up (Table 2 and Table 3).

Clutch sizes were compared among islands in 1991, 1995, 1996 and in 1997 (limited data in 1992 and 1994, Table 3). In 1991 and 1995, average clutch size was similar on all islands (ANOVA, 1991: $F = 1.72$, $df = 4, 117$, $p = 0.15$, 1995: $F = 0.98$, $df = 4, 214$, $p = 0.42$). In 1996, the average clutch size was largest on Storholmen (ANOVA, $F = 2.81$, $df = 3, 180$, $p = 0.04$, Table 3) and in 1997, average clutch size was largest on Eskjer (ANOVA, $F = 2.66$, $df = 5, 270$, $p = 0.02$, Table 3). A seasonal decline in clutch size of barnacle geese has been found in the Kongsfjorden colony (Dalhaug et al. 1996) where late-nesting females allocated fewer body reserves into eggs. This is advantageous because late-nesting females have a shorter period to regain body reserves after incubation. In a study from the same area on common eiders, clutch size was found to be negatively correlated to the time of egg-laying (Mehlum 1991b). An early break-up of sea ice may therefore result in larger clutches, although in 1996 and 1997 most islands were free of sea ice early. Accordingly an early break-up of sea ice is not the only explanation for larger clutches at Storholmen and Eskjer in 1996 and 1997. Age

distribution of the breeding birds could be an alternative explanation (see above).

Including all years and nest locations, no significant correlation between average clutch size and total number of nests on the islands were found (linear regression, all islands: $R^2 = 0.14$, $n = 23$, $p = 0.08$, all islands except Storholmen in 1993 (over-represented with young breeders): $R^2 = 0.02$, $n = 22$, $p = 0.5$). Moreover, including nest site and year in addition to total nest number on the island in the model, none of the variables seemed to determine clutch sizes (GLM, Type III sum of squares, all p-values > 0.5). The traditional theory is that clutch size in arctic-nesting geese is determined by processes going on before the nests are established; namely by available body reserves at the start of egg laying (Lack 1967; Ryder 1970; Ankney & MacInnes 1978; Ankney et al. 1991). Several studies have also presented evidence that clutch size in precocial birds is ultimately determined by the interaction between the use of body reserves for egg production and later use for incubation and care of young (Gloutney & Clark 1991; Erikstad & Tveraa 1995; Tombre & Erikstad 1996). The geese in this colony also spend a considerable amount of time feeding elsewhere before they arrive at Ny-Ålesund and feeding conditions before arrival are therefore crucial to their reproductive success (Tombre et al. 1996). However, early breakup of sea ice may contribute to early egg laying and larger clutches, and, in addition to the presence of foxes, this could proximately influence breeding conditions on the different islands in Kongsfjorden.

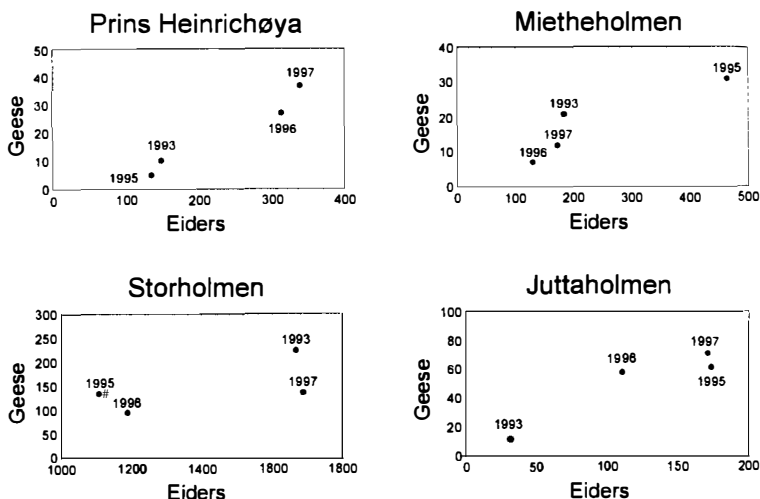


Fig. 3. Breeding numbers of common eiders and barnacle geese of four islands in 1993 and 1995–1997 in Kongsfjorden, Svalbard.

Table 4. Percentage of barnacle goose nests in relation to common eider nests on four islands in Kongsfjorden, Svalbard (see Fig. 3 for sample sizes).

Year	Prins Heinrichøya	Mietheholmen	Storholmen	Juttaholmen
1993	11.4	6.8	13.4	7.4
1995	6.7	3.7	12.1	4.4
1996	5.4	8.6	7.9	4.7
1997	6.9	10.9	8.1	7.6

Barnacle goose nests and common eider nests

In Fig. 3, the numbers of barnacle goose nests on four important breeding locations in 1993 and 1995–1997 are plotted against the numbers of common eider nests on each location during the same years. The variation between years in nest numbers is considerable, and there is obviously a positive correlation between the number of nests on the different islands for the two species (although sample sizes are too small to perform a statistical test). Good breeding conditions for geese are also good breeding conditions for common eiders, presumably reflecting the sea-ice conditions and the islands' availability for nesting. Comparing the percentage of goose nests in relation to common eider nests, the number of goose nests does not seem to have increased at the expense of common eider nests over the last five years (Table 4). Accordingly, no obvious competition for nest sites was found between the two species.

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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 $N = r * \Sigma n_i / \Sigma m_i$. 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 ($\Sigma n_i / N$) 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_{fledg}) 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_{fledg} .

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 $\phi_{sat} \cdot p_{sat}$ to $\phi \cdot p$ 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	$0.98166 + 0.00033 \cdot \text{day}$

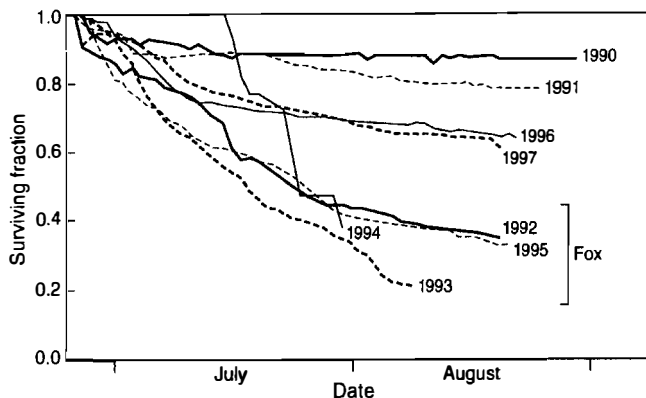


Fig. 1. The surviving fraction of goslings against date for different years. The surviving fraction is calculated by multiplying daily survival rates. There is a clear distinction between years with and without arctic foxes.

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)	n	avg	(st. dev)	n			
1990	3.27	(1.41)	41	3.13	(1.44)	40	1	2	24 Aug
1991	3.56	(1.38)	66	3.19	(1.40)	64	2	3	17 Aug
1992	3.25	(1.82)	84	2.00	(1.26)	57	27	32	16 Aug
1993	2.96	(1.14)	116	1.88	(1.23)	64	52	45	3 Aug
1994	1.91	(0.90)	11	1.67	(0.94)	6	5	45	27 July
1995	3.10	(1.37)	172	2.33	(1.32)	129	43	25	8 Aug
1996	3.28	(1.17)	174	2.96	(1.32)	160	14	8	17 Aug
1997	3.32	(1.05)	121	3.01	(1.19)	102	19	16	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

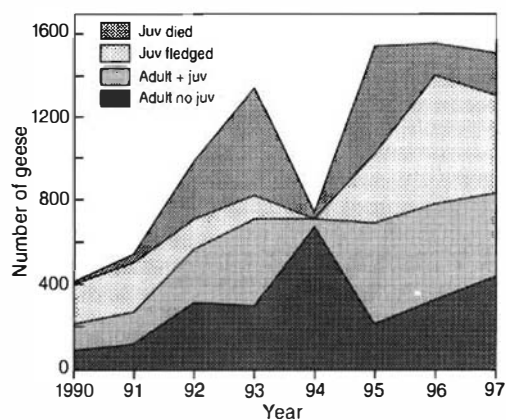


Fig. 2. The development of the barnacle goose population in Kongsfjorden, based on Petersen estimates. The adult birds are divided in those with and without hatching goslings. The number of goslings is divided in those dying before fledging and those surviving until fledging.

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	$S_{\text{hatch-first}}$	Number of goslings at hatching	$S_{\text{first-catch}}$	Number of goslings at catching	$S_{\text{first-fledg}}$	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	Adult
1990	0.24 [0.08,0.54] _a	0.90 [0.74,0.96] 0.88 [0.76,0.95]	0.23 [0.08,0.52] _a	0.85 [0.68,0.94] 0.99 [0.75,1.00]	0.65 [0.25,0.91]	0.93 [0.82,0.97] 0.92 [0.85,0.96]
1991						
1992	0.38 [0.28,0.48]	0.93 [0.86,0.97] 0.88 [0.82,0.93]	0.88 [0.78,0.94] 0.50 [0.36,0.64]	0.91 [0.83,0.95] 0.96 [0.91,0.99]	0.78 [0.69,0.86] 0.59 [0.43,0.73]	0.86 [0.81,0.91] 0.85 [0.81,0.88]
1993	0.38 [0.24,0.55]	0.81 [0.75,0.86] 0.83 [0.77,0.87]	0.40 [0.24,0.57] _b	0.83 [0.78,0.88] 0.81 [0.76,0.86]	0.81 [0.55,0.94]	0.88 [0.85,0.91] 0.89 [0.85,0.92]
1994	0.27 [0.13,0.49] _b	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]
1995						
1996	0.39 [0.26,0.55]					

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

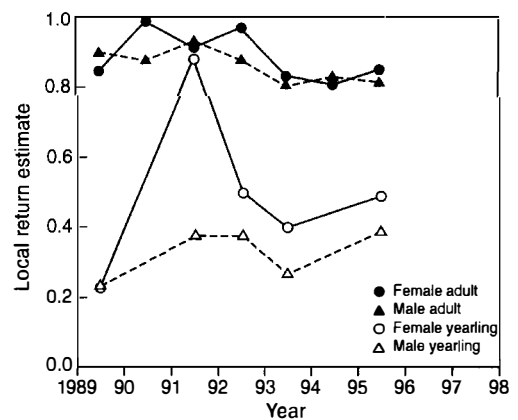


Fig. 3. Local return rate of barnacle geese to the Kongsfjorden area in different years, per sex and age.

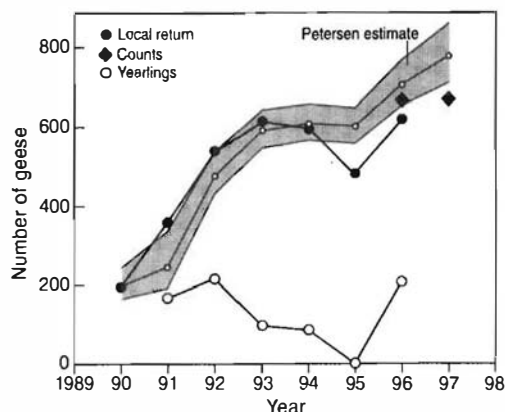


Fig. 4. The barnacle goose population in Kongsfjorden. Petersen estimates for each year are compared with a population trend based on local return rates and gosling production. In 1996 and 1997, the number of adults was also counted in the entire fjord (◆).

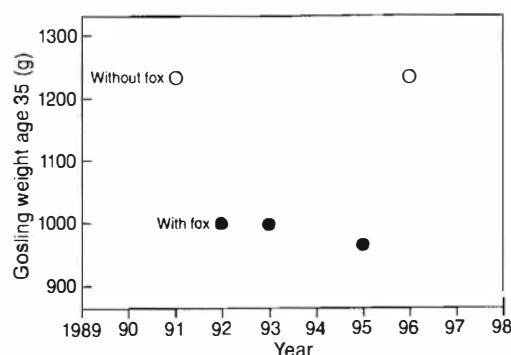


Fig. 5. Body mass of goslings at age 35 days in different years as calculated from growth curves. In years without arctic foxes, body mass is over 200 gram heavier than in years when arctic foxes are present.

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

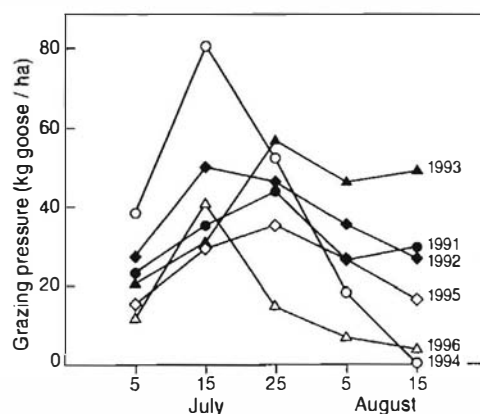


Fig. 6. Grazing pressure of barnacle geese on the shore of the lake, Solvatnet, the site with the highest goose density in Kongsfjorden. Grazing pressure is expressed as the combined body mass of adults and goslings present.

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

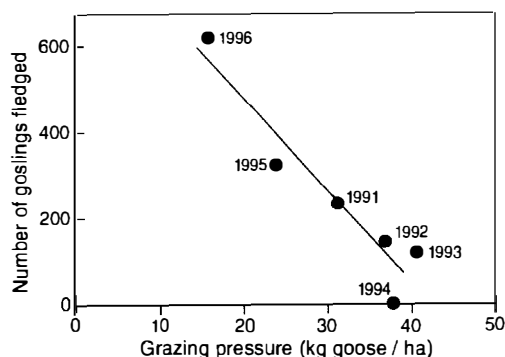


Fig. 7. A negative relation between the number of goslings produced and the grazing pressure on the mossy shore of the lake, Solvatnet ($F_{1,4} = 35.94$, $P = 0.004$). When the geese are able to use the tundra and rely less on the vegetation close to water, the total production of goslings in the colony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

Juvenile survival = juvenile autumn survival \times juvenile return rate,

Reproduction rate = (clutch size \times 0.5) \times egg survival \times early gosling survival \times 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

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

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

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

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:

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

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

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

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

$$\text{AE-coefficient} = \text{CV}_i \times E_i$$

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.

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Effects of predation risk on site selection of barnacle geese during brood-rearing

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Stahl, J. & Loonen, M.J.J.E. 1998: Effects of predation risk on site selection of barnacle geese during brood-rearing. Pp. 91–98 in Mehlum, F., Black, J.M. & Madsen, J. (eds.): Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skrifter* 200.

Barnacle geese *Branta leucopsis* breed on small islands in the Kongsfjorden area, Spitsbergen. Shortly after hatching, families approach feeding sites at the mainland coast in the close surroundings of the village Ny-Ålesund. The goslings are subject to predation by arctic foxes *Alopex lagopus* throughout the whole brood-rearing period. This study compares the choice of foraging areas in a year with fox predation with years with no foxes present. Observations of ringed individuals show that the use of tundra sites by families decreases in a year with foxes present. In such a year, foraging of goose families is limited to sites in the proximity of open water. Non-breeders are not affected in their choice of foraging areas by the presence of arctic foxes and prefer sites along lake shores during wing moult. Habitats vary in food quality and quantity according to the dominant vegetation type. Approximately 85% of the diet of geese grazing on meadows within the village and on tundra sites consists of graminoids and dicots, whereas geese grazing on lake shores consume up to 35% moss. A grass-dominated diet yields good digestibility and a favourable protein gain, compared to moss which is of lower quality. In a fox year, predation risk restricts goose families to a small range of safe foraging sites where grazing pressure is high. Data on slower gosling growth support the hypothesis of food limitation and competition among families in such a year.

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Introduction

In high arctic breeding grounds, many goose species are confronted with substantial constraints concerning favourable food sources. Because of the shortness of growing seasons at high latitudes, the productivity of arctic grassland ecosystems is low (Gauthier et al. 1997). Plant cover is often patchy and potential food plants vary considerably in quality; digestibility and protein content of food plants increase from moss to dicots to monocots (Prop & Vulink 1992; Prop & de Vries 1993). Grass species rank highest in crude protein content (15–25%) and in digestibility (up to 60%); mosses only yield 10% crude protein and are highly indigestible due to a fibre content of 80% (Staaland et al. 1983; Prop & Vulink 1992; Gaddalah & Jefferies 1995). Although a graminoid-based diet is desirable for non-breeders and family birds alike, Prop & Vulink (1992) showed that adult geese coped with high moss contents in their diet by prolonged food retention. During the continuous light regime of the arctic sites, adult barnacle geese *Branta leucopsis* increased the

retention time of ingested food and thereby raised digestibility.

The circumstances are different for geese which raise goslings. Gosling growth of different goose species has been shown to be susceptible to slight changes in food quality (Lindholm et al. 1994; Gadallah & Jefferies 1995) and availability of favourable food plants (Cooch et al. 1993). In addition, growth conditions during the gosling period affect adult size and survival (Owen & Black 1989; Sedinger et al. 1995; Loonen et al. 1997; Loonen et al. in press). The small digestive tracts of goslings are neither able to cope with long retention times during food processing (Sedinger & Raveling 1988) nor can they compensate for low nitrogen contents of food plants by increasing their intake (Manseau & Gauthier 1993). Therefore, family birds must mainly feed on nitrogen-rich forage with low fibre content as is provided by a grass-dominated diet.

The short, high arctic summer and approaching autumn migration require profitable foraging decisions to be made by all arctic breeding geese during the moulting and brood-rearing periods.

Predation risk is one important parameter that affects these foraging decisions. Predators influence the fitness of individuals either directly by attacking the offspring or the individuals themselves, or indirectly by affecting the relative accessibility of foraging sites (Lima & Dill 1990). Arctic foxes and glaucous gulls *Larus hyperboreus* are considered important predators in northern ecosystems (Mehlum 1991; Stickney 1991; Birkhead & Nettleship 1995). Syroechkovskiy et al. (1991) discuss the breeding success of different arctic goose species and lemming-cycle-related predation pressure by foxes in northern Russia. In a colony of Alaskan breeding black brant *Branta bernicla nigricans*, nesting success was increased by removal of foxes from the area (Anthony et al. 1991). Most of the above-mentioned studies, however, focus on the direct influences of predators on breeding performance and hatchling mortality. Little is known about the influence of predation on the choice of foraging areas in terrestrial ecosystems (see Lima & Dill 1990). Our study concentrates on the indirect effects of the presence of a predator in an area. We compare the habitat use of barnacle geese in years with and without predation by arctic foxes. This comparison is possible in the Kongsfjorden colony due to the philopatry of family birds as well as non-breeders to a limited area of 10 km² during brood-rearing and wing moult.

Study area

This study was carried out in the surroundings of the village Ny-Ålesund in Kongsfjorden (78°55'N, 11°56'E) on the island of Spitsbergen in the Svalbard archipelago (Fig. 1). The study area (10 km²) is bounded by the fjord to the north, by mountains to the south and by glacial gravel fields to the east and west. It comprises different vegetation types which can be grouped into three habitat types:

(1) *meadows*, which are characterised by a well-drained sandy soil and dominated by grasses such as *Poa arctica* and *Deschampsia alpina* (total area 0.05 km²). This habitat type can only be found in the centre of the village.

(2) *lake shores*, which are characterised by a wet undrained soil and dominated by moss

vegetation with sparse stands of *Poa arctica* (total area 1.34 km²).

(3) *tundra*, which is characterised by lichens and dicots such as *Salix polaris* and *Saxifraga oppositifolia* and scattered stands of various monocotyledons (total area 6.14 km²). This dominant habitat type is located in a band of an average width of 1 km between mountains and fjord.

The barnacle goose breeding colony in Kongsfjorden was established in the early 1980s (Prestrud et al. 1989). In 1996, a count resulted in approximately 700 adult geese (Loonen et al., this volume). To evade predation by arctic foxes, most of the geese nest on small islands in the fjord. Goslings hatch during the first two weeks of July, with peak hatching around 7 July (Tombre 1995). Families approach feeding sites along the mainland coast within the first week after hatching. Groups of families and of moulting non-breeders concentrate in the close vicinity of the village and surrounding tundra throughout the whole moulting and brood-rearing period in July and August.

Methods

Observations on ringed individuals

Since 1987, barnacle geese of the Kongsfjorden colony have been caught during wing moult and marked individually with coded colour leg rings (Loonen et al., this volume). The majority of the breeding pairs is recognisable by leg rings of at least one partner. The data analysed in this paper were collected during the months of July and August of the years 1991, 1993 and 1996. On a daily basis, ring readings of all geese present in the focal study area (2 km² in the vicinity of Ny-Ålesund) were carried out. The rest of the study area was covered during weekly censuses. Recorded parameters for ringed birds were family status and used habitat type.

Predation pressure

Post-hatching predation of goslings by arctic foxes on the mainland shore varied considerably

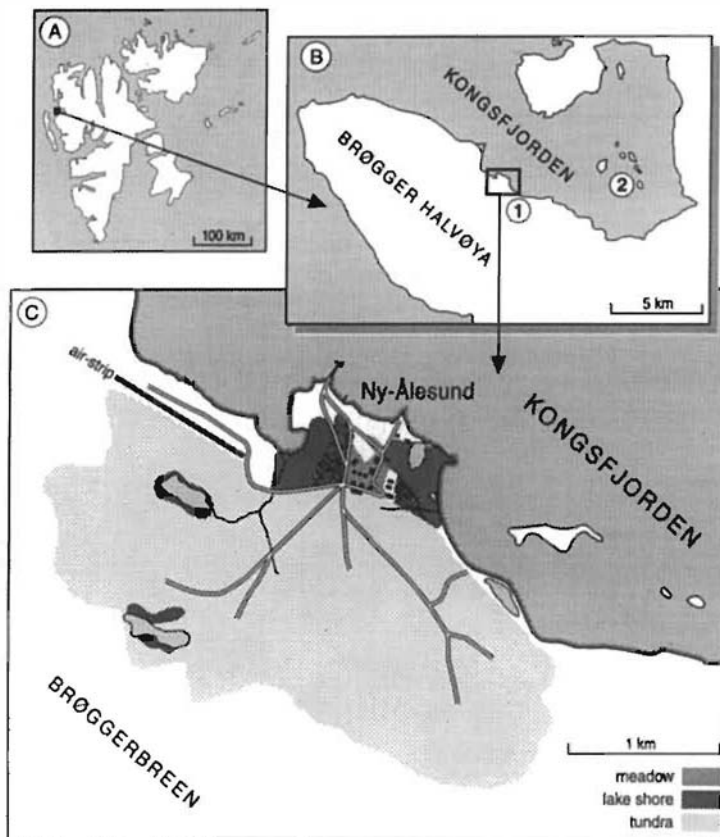


Fig. 1. The study site. A. Svalbard. B. Kongsfjorden with the village Ny-Ålesund ① and the breeding islands ②. C. Focal study site with three distinguished habitat types.

between years. In 1991 and 1996, no foxes were recorded in Kongsfjorden. We refer to these years as fox-free. In 1993, at least three foxes were observed on the southern side of Kongsfjorden and one den was found. However, no foxes approached the main breeding island and the hatching success of the geese was hardly affected by fox predation. To calculate the influence of fox predation on the fledging success of goslings, we compared family sizes of ringed individuals at their first sighting on the mainland shore in July with family sizes of the last sighting in August. This method corrects for early hatchling predation by glaucous gulls on the breeding islands.

Vegetation sampling and dropping analysis

We measured the standing crop of graminoids by using a semi-random sampling technique whereby

five samples were collected per sampling effort in all three habitat types. Within a movable metal frame (covering an area of 20 by 20 cm), all grass shoots were clipped, sorted into living and dead material, dried for 48 h at 60°C in a drying stove and weighed. Differences in species composition of graminoid standing crop among the three habitats were not taken into account and we refer to all species collectively as monocots in this study.

For dietary analysis five faeces samples each containing five droppings of adult geese were collected in all three habitat types concurrently with measurements of graminoid biomass. The samples were dried for 48 h at 60°C, blended and washed over a 0.1 mm sieve. At random, 100 cell fragments were microscopically determined to genus level and measured in size. The composition of the diet was determined according to the occurrence and the size of plant fragments. These surface measurements of plant fragments in the

Table 1. Brood rearing success of ringed female barnacle geese in the period from hatching to fledging. (1991 and 1996 without fox predation (-), 1993 with fox predation (+))

Year	Total number of females	Successful (all young fledge) %	Partly successful (some young fledge) %	Failed (no young fledge) %
1991 -	60	62	35	3
1993 +	90	13	42	45
1996 -	100	79	16	5

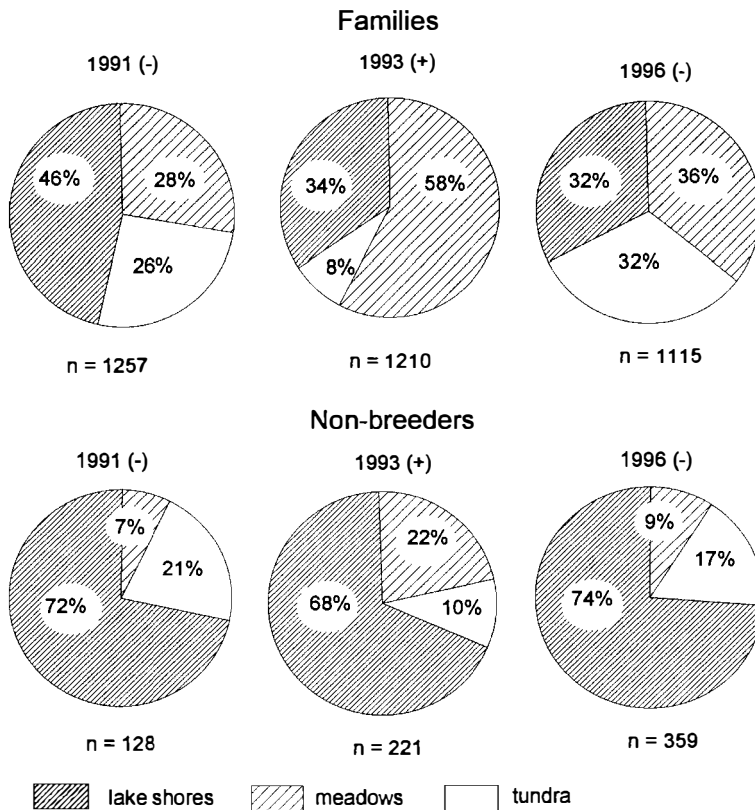


Fig. 2. Habitat use of families and non-breeders in three years: 1991 and 1996, fox-free years (-), and 1993, fox predation year (+).

diet counterbalance differential fragmentation of plant species in the goose gut (for technique see e.g. Owen 1975). During further analysis, food species were grouped as monocots, dicots and mosses. Data on standing crop and goose diet were collected in the first week of August 1997, when non-breeders and families were both present on the mainland sites in the breeding season.

Habitat availability and safety

By means of an OTT planimeter, the surface areas of the three habitat types used were measured on vegetation maps (Brattbakk 1981a, b) and on false colour satellite pictures. The distances of the different habitat types from the respectively

Table 2. Extrapolation of available grass biomass for brood-rearing areas for barnacle geese in Ny-Ålesund, Spitsbergen. Data are based on Figs. 2 and 3B.

Year	Area type	Area size and availability	Grass biomass (dry weight)
1991	Meadows	5.4 ha	27.16 kg
	Lake shores	134.2 ha	150.84 kg
	Tundra	613.7 ha	1669.26 kg
	Total	753.3 ha	1847.26 kg
1993	Meadows	5.4 ha	27.16 kg
	Lake shores	134.2 ha	150.84 kg
	Tundra	0 ha	0 kg
	Total	139.6 ha	178.00 kg
1996	Meadows	5.4 ha	27.16 kg
	Lake shores	134.2 ha	150.84 kg
	Tundra	613.7 ha	1669.26 kg
	Total	753.3 ha	1847.26 kg

closest water body in all areas were measured on the same maps. Maximum and minimum distances contributed to the values shown in Fig. 3A.

Data analysis

To analyse the data on area use, we included observations of female birds from the period of 15 July (8 days after the hatch peak on the breeding islands) to 15 August (before non-breeders left the area). We accounted for an interval of at least 12 hours between repeated sightings of the same ringed bird to enable individuals to move among habitat types, and we assumed independence between these observations. Repeated sightings of the same individual within a shorter time period were not included in the analysis. Birds were classified as family birds if they had a partner and were accompanied by at least one gosling. The category 'non-breeders' was applied to geese with or without a partner and which were neither accompanied by goslings nor registered as 'breeding birds' from censuses on the breeding islands (Tombre, unpubl. data). Failed breeders, which lost all young within the period from hatching to fledging, were not included in the analysis.

Statistical analysis

Chi-square statistics were applied to the data on the habitat use of ringed birds. Data on standing crop were log-transformed and tested using a one-way ANOVA and Tukey test. For analysis of differences in diet composition between areas, a one-way ANOVA and Tukey test were applied to the weighed data. For statistical analysis the program SPSS/PC+ was used.

Results

Influence of fox predation on fledging success

Table 1 compares the breeding success of female geese in two fox-free years (1991 and 1996) with that of a typical fox year (1993). In the fox year, 45% of the females had lost their goslings by the end of the brood-rearing period. Another 42% of the families were reduced in size. Only 13% of all females raised the entire brood size successfully. In fox-free years, respectively 62% or 79% of all females raised the entire number of goslings successfully.

Habitat choice of families and non-breeders

Table 2 presents data on the size of the available areas in different years (assuming that tundra sites are inaccessible in fox years). The available foraging area is five times larger in fox-free years. Area use of families varied significantly between a fox year and fox-free years (Fig. 2A, 1993 vs. 1991: $\chi^2 = 252.0$, $df = 2$, $p < 0.001$; 1993 vs. 1996: $\chi^2 = 222.9$, $df = 2$, $p < 0.001$). In 1996, a year without foxes, families used meadows, tundra sites and lake shores equally as foraging sites. In 1993, a fox year, the use of tundra sites was restricted to 8% of all family sightings. The use of lake shores remained approximately the same, but the utilisation of meadows increased by almost 20% in a fox year. Moulting non-breeders used mainly lake shore vegetation for foraging, and only 30% of all sightings accounted for the two other habitat types (Fig. 2B). Non-breeders also tended to switch from meadow sites to tundra areas in fox-free years, though these habitats were never preferred as much as by family birds (1993 vs. 1991: $\chi^2 = 17.9$, $df = 2$, $p < 0.01$; 1993 vs. 1996: $\chi^2 = 24.5$, $df = 2$, $p < 0.01$).

Safety, food availability and dietary considerations

The predation risk of the three habitat types was indicated by the distance of foraging sites from the nearest water body (Fig. 3A). Flightless geese had to cover a distance five times greater when escaping from a fox on tundra sites compared to geese feeding on the meadows. The average biomass was low (less than 1 g/m²) in all three habitat types, and the harvestable standing crop of monocots was not significantly different between meadows, tundra sites and lake shores (Fig. 3B, one-way ANOVA, $p > 0.05$).

For geese foraging on meadow or tundra sites, approximately 80% of the diet consisted of monocots (Fig. 3C). Along lake shores, grasses formed only 50% of the food and mosses accounted for 30% of the diet. The fraction of monocots in the goose diet on meadows and on the tundra differed significantly from that on lake shore vegetation (one-way ANOVA, Tukey test,

$F_{2,15} = 14.89$, $p < 0.001$). Dicots played a minor role as a food source in all three habitat types.

Discussion

Fledging success in fox years versus fox-free years

A between-year comparison of the number of females that lost all their young between hatching and fledging reveals that arctic foxes were likely the main cause for this failure. In fox-free years, only a small percentage of families, which managed to escape gull predation on the breeding islands and reached the foraging sites on the mainland, failed completely (Table 1). Families were very vulnerable to fox predation throughout the whole brood-rearing period (own obs.) and were alert for access to possible refuge areas (mainly the water bodies of shallow lakes) whenever arctic foxes approached.

Area choice and dietary considerations of non-breeders

Moulting non-breeders preferred mossy lake shores as main foraging habitat irrespective of the presence of foxes throughout the years (Fig. 2). These areas offered the lowest biomass of monocots compared to the other two habitat types, and dropping analysis revealed a high fraction of mosses in this diet. It is possible, however, that this group of adult geese can compensate for the low digestibility of mosses with a prolonged retention time (Prop & Vulink 1992), allowing them at the same time to profit from the close proximity of the lakes as refuges during their flightless period (Fig. 3A). In addition, non-breeding birds enter the flightless period with better body condition than breeders (unpubl. data) and thus have an energetic margin in balancing their budget. This preference of safety over more favourable conditions represents a trade-off which deserves more detailed study.

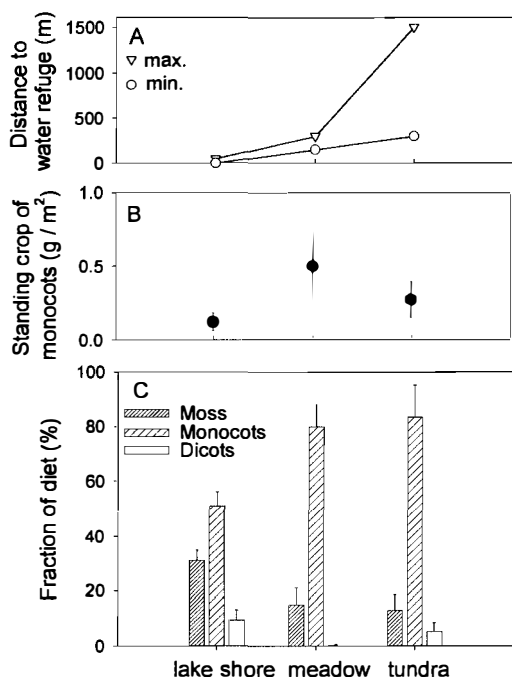


Fig. 3. Site characteristics and goose diet for the three habitat types. A. Maximum and minimum distance to nearest water body. B. Standing crop of living grass biomass (mean, SE, $n = 5$). C. Fraction of the three main food classes in the diet (mean, SE, $n = 5$).

Area choice and dietary considerations of families

In all years, mossy lake shore sites account for less than 50% of all sightings of families. Accordingly, families use either tundra or meadow sites in more than 50% of all cases. Both these sites contain vegetation types that grant a graminoid-based diet. The shift of family birds toward tundra sites in fox-free years suggests a strong restriction in years with fox presence to limited, but safe, areas in the proximity of village houses and along lake shores. The available grass biomass on tundra sites is as sparse as on mossy lake shores. The geese, however, seem to be able to compensate for the low standing crop on the tundra and achieve a favourable graminoid-based diet there (Fig. 3C). They most likely forage highly selectively on monocot shoots and make use of the much larger tundra area (Table 2). If we calculate the mean monocot biomass measured in the three habitat types (Fig. 3B) for the whole area

size accessible under the two predation scenarios, the calculation results in a 10 times larger amount of available food in years without foxes.

Consequences

Several studies have shown that growing goslings are especially vulnerable to shortages in food availability and quality (e.g. Aubin et al. 1986; Gadallah & Jefferies 1995). Based on results from a supplementary feeding trial with semi-captive goslings of greater snow geese *Anser caerulescens atlantica*, Lindholm et al. (1994) argue that a five to seven day difference in hatching date results in major consequences for growth and survival of the young. In greater snow geese, late broods are faced with a rapid decline in availability and quality of the major food plants during the arctic summer. In addition, late families are probably excluded from favourable foraging sites through mechanisms of intraspecific competition (Dalhaug et al. 1996 for barnacle geese). Hughes et al. (1994) suggest from their study on greater snow geese that experienced, early laying females stay at one foraging site during brood-rearing and force late hatching families to wander to other areas. Our own data suggest a link between predation, restricted area accessibility and intra-specific competition. The aspect of competition is also emphasised by another study on the Kongsfjorden goose population (Loonen et al., this volume). The authors show there that goslings of similar age are approximately 250 grams heavier in years without fox predation than in fox years. The early exhaustion of favourable but limited meadow sites and the absence of alternative foraging areas in a fox year are explanations for the observed weight differences. In a study on lesser snow geese *Anser caerulescens caerulescens*, dispersal behaviour in reaction to deteriorating environmental conditions is advantageous (Cooch et al. 1993). Breeding pairs respond to overcrowding and vegetation degradation in a traditional breeding colony by colonising a new breeding site where they are able to raise heavier and larger goslings. Our study indicates that the presence of a predator in a brood-rearing habitat can reinforce competition and evoke density dependent processes similar to overcrowding in large breeding colonies.

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Does arctic vegetation change when grazed by barnacle geese? A pilot study

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The effects of grazing by barnacle geese *Branta leucopsis* on arctic vegetation was studied. Two plots where grazers had been excluded five and six years previously were compared with grazed vegetation nearby. The excluded plots contained more live biomass than the area with grazed vegetation. However, there was no significant difference in density of shoots and number of leaves per shoot in the heavily grazed *Poa arctica*. Within the excluded plots, there was a slow build-up of dead material and the moss carpet had grown thicker than in the grazed plots. The number of inflorescences was the most prominent feature, which differentiated the excluded vegetation from the grazed surrounding. There is no evidence for habitat deterioration caused by increased grazing pressure from the expanding barnacle goose population as has been reported for the snow goose on the Hudson Bay lowlands in Canada. The increased activity of nitrogen fixation by cyanobacteria in grazed vegetation might be a mechanism which compensates for the nitrogen deficit caused by the migratory geese.

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Introduction

Increasing numbers of lesser snow geese *Anser caerulescens caerulescens* in the southern region of Hudson Bay, Canada, are destroying their grazing habitat (Kotanen & Jefferies 1997; Jano et al. 1998). During snow-melt, the geese grub and destroy large areas of vegetated salt marsh in search for rhizomes. In the open areas salinity increases, which hampers revegetation (Srivastava & Jefferies 1996). This large-scale destruction of sub-arctic habitat has led to an increasing effort to reduce the size of the present population of the mid-continental lesser snow goose (Ankney 1996).

In the same area it is shown that goose grazing during summer can have a positive effect on vegetation production. The frequently produced goose droppings are a source of nitrogen for the nitrogen-poor vegetation, and the production of grasses and sedges eaten by the geese is enhanced because of the acceleration of the nitrogen cycle (Bazely & Jefferies; Hik & Jefferies 1990). The exporting of nitrogen out of the ecological system by the autumn migration of the newly produced goslings is compensated by the enhanced nitrogen fixation of cyanobacteria in the grazed vegetation (Bazely & Jefferies 1989).

In areas that are located more to the north, no positive effect of goose grazing on plant production has been found (Gauthier et al. 1995; Bakker & Loonen 1998). Here, less grubbing by geese is observed and not all goose-grazed areas are situated on salt marshes. Fresh water lake areas and tundras, where salt stress is absent, are also used. However, the great increase in most goose populations since 1970 has caused a growing concern about the effect of the increase on arctic vegetation and associated wildlife. In the High Arctic, after the geese have migrated out there is less time for the area to recuperate from grazing because of the short summer.

The effects of grazing by the barnacle goose *Branta leucopsis* have been examined at two sites. At each site, a plot where grazing by geese had been excluded for many years was compared with grazed vegetation nearby.

Material and methods

The study was performed in the direct vicinity of the village of Ny-Ålesund, where barnacle geese have been grazing since 1980. The number of



Fig. 1. The enclosure on site A, built in 1993 and photographed in 1998.

barnacle geese at this study area has been steadily increasing, together with the entire population of Svalbard barnacle geese (Loonen et al. 1998, this volume). Two 0.7 m² enclosures were defined, one in 1992 and one in 1993. These enclosures survived until 1998 when the vegetation inside the enclosures was then compared with grazed control plots directly outside the fence. We assume that there was no difference on either side of the fence in microclimate or timing of snowmelt and that any difference between the vegetation inside and outside of each enclosure is caused by grazing only. The enclosure built in 1993 on site A was situated in a wet, moss area at a site where shoots of *Poa arctica* were relatively abundant (Fig. 1). The enclosure built in 1992 on site B was built on a slightly dryer area, where *P. arctica* also dominated. No bare ground was present in either of the vegetation types. All vascular plants protruded through a completely closed moss carpet. Both sites were heavily grazed by barnacle geese during the summer period and had vegetation types comparable with, respectively, the moss areas and the meadows in Stahl & Loonen (1998, this volume).

On 11 August 1998, the vegetation was described at both sites. Sixteen randomly placed frames (5 × 5 cm²) were placed both inside and outside the enclosed plot. The following seven parameters were measured in each plot: (i) Coverage of live biomass of *P. arctica* (percentage); (ii) Coverage of dead biomass of *P. arctica* (percentage); (iii) Density of shoots of *P. arctica* (calculated as density per m²); (iv) Length of all live leaves per shoot of *P. arctica* (mm per shoot); (v) Number of live leaves per shoot of *P. arctica*;

(vi) Width of a full-grown *P. arctica* leaf (mm); (vii) Coverage of other plant species (all dicots; percentage).

Furthermore, the following three parameters were measured once per area: (i) Total number of live inflorescences of *P. arctica* per m²; (ii) Total number of live inflorescences of dicots per m²; (iii) The maximum difference in height of the moss carpet inside the enclosure, compared to the grazed environment from a lateral view.

The nitrogen fixation activity of cyanobacteria present on the vegetation was measured by collecting two times five samples of vegetation with a surface area of 1.13 cm² on each site and measuring ethylene formed by incubating the vegetation samples for 3 h in daylight at 20°C in 10 ml vials with 10% acetylene in the atmosphere as described in Solheim et al. (1996). Nitrogen fixation activity was expressed as nmol ethylene produced h⁻¹ cm⁻² vegetation.

The difference between enclosed and grazed vegetation in each site was tested by Mann-Whitney U-tests.

Results

Two years after the enclosing, the most prominent feature in the enclosures was the presence of numerous inflorescences. This was still the case in 1998, when site A had been enclosed for 5 years and site B for 6 years (Table 1). The standing crop of *P. arctica* was considerably larger inside the enclosures than outside. Both the coverage and the total leaf length per shoot were significantly higher inside the enclosures. There was also a clear build-up of dead material in the standing crop within both enclosures. No difference was evident in the number of shoots per m² and the number of leaves per shoot, suggesting little effect of grazing on the occurrence of *P. arctica*. However the grass leaves in the enclosed plots were broader than in the grazed control plots.

Site A had fewer vascular plant species than site B. At site A, *P. arctica*, *Saxifraga cernua* and *Ranunculus hyperboreus* were present in the enclosure, and *P. arctica* and *R. hyperboreus* were present in the grazed area. At site B, *P. arctica*, *Deschampsia alpina*, *S. cernua*, *Saxifraga cespitosa*, *Cerastium arcticum*, *Cardamine nymanii* and *Polygonum viviparum* were present in the exclo-

Table 1. Comparison of grazed plots with plots which have been exclosed for at least five years from grazing. For a full explanation of the variables and the units of measurement see the Material and methods section. Significance is based on a Mann-Whitney U-test: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; n.s.: not significant; "no test, $n = 1$ "; ^b: $n = 5$; all other comparisons: $n = 16$.

		<i>Poa arctica</i>							Didcot		
		Coverage (%)		Shoot number (m ⁻²)	Total leaf length (mm)	Leaves per shoot	Leaf width (mm)	Inflorescences (m ⁻²)	Coverage (%)	Inflorescences (m ⁻²)	N fixing activity (nmol C ₂ H ₄ h ⁻¹ cm ⁻²)
Site		Live	Dead								
A	Exclosed	29.7	5.8	8320	164	3.1	2.0	108	5.5	5	0.7
	Grazed	10.8	1.4	9720	31	3.0	1.1	0	0.1	0	2.6
	Significance	***	***	n.s.	***	n.s.	*	a	**	a	** ^b
B	Exclosed	17.1	11.9	3760	70	2.8	2.5	2	18.3	410	0.5
	Grazed	4.1	0.3	3680	18	3.0	1.5	0	15.6	72	1.2
	Significance	***	***	n.s.	***	n.s.	*	a	n.s.	a	n.s. ^b

sure and *P. artica*, *Sagina cernua*, *S. cespitosa*, *C. nymanii* and *S. nivalis* were present in the grazed area. Most plants were growing in small tussocks except *P. artica* and *S. nivalis*. At site A, *Calliergon richardsonii* was the most dominant moss species, while at site B, *Sanionia uncinata* was dominant, but several other moss species were also present. At site A the moss surface had grown almost 50 mm higher in the exclosure than in the grazed environment. For site B, this difference was only 2 mm.

At both control sites the grazed vegetation had a higher level of nitrogen fixation by cyanobacteria than the exclosed vegetation, though the difference was only significant at site A.

Discussion

Though *P. artica* was grazed intensively during summer on the tundra around Ny-Ålesund and 66% of the annual production was removed by the geese (Bakker & Loonen 1998), there was no long-term effect of goose grazing on the occurrence of *P. artica* as measured in the density of shoots and the number of leaves per shoot. Grazed plots had a lower standing crop (measured as percentage cover and as total leaf length per shoot), but this was mainly due to recent grazing in 1998.

The build-up of dead material was a prominent feature in the exclosed plots. In the grazed plots, dead material was rare because most leaves were

eaten before senescence occurred, resulting in a reduced flow of senescing tissue (Bakker & Loonen 1998). Dead material may eventually hamper vegetation growth due to reduced light availability, as shown by Wegener and Odasz (1997) in a pot experiment, though this was not evident after 6 years in our field study.

The flowering of *P. artica* and various dicots was also a prominent feature in the exclosures. The seeds and flowers of most plants were favoured food items for the barnacle geese (own obs.), but flowering was rare in the grazed vegetation. The flowering may enhance the fitness of the plants, though vegetative propagation and clonal growth are common alternatives for establishment in arctic plants (Chou et al. 1992).

Grasses in the exclosed plots had substantial broader leaves. This might be the result of less nutrients being taken from the plant. The reserves stored in the roots of the arctic plants are important for future production and the amount of nutrients stored is related to the amount of above-ground biomass (Archer & Tieszen 1983). Both the appearance of thicker leaves and the flowering became obvious when the exclosures were two years old, and were still visible after six years of exclusion.

At both study sites, there were more plant species growing in the exclosures than in the grazed plots. A similar effect was also observed in the snow goose study of Bazely and Jefferies (1986).

The fact that barnacle geese also feed on moss resulted in a difference in height of the moss

surface level in and outside the exclosures. It is not clear if an interaction existed between the moss and the vascular plants which could be affected by the grazing.

Nitrogen fixation is an expensive physiological process. Only when nitrogen is limiting does cyanobacteria transform atmospheric nitrogen into ammonia. In areas where nitrogen was abundant (for example under bird cliffs in the Arctic where the vegetation was fertilised by the faeces of seabirds), nitrogen fixation was never found even though the bacteria were usually present (Solheim et al. 1996). In grazed areas, there is a net export of nitrogen by migratory barnacle geese because nitrogen is deposited in the goose body. The females increase about 300 grams in weight while recuperating from the incubation period, and the goslings grow from 70 grams to 1,250 grams (own obs.). Around 15 August, at the end of the moulting period, the goslings fledge and the barnacle geese leave the study area in preparation for migration to Scotland. The response of the cyanobacteria to the scarcity of nitrogen at the heavily-grazed moulting site was increased nitrogen fixation. This mechanism compensated for the removal of nitrogen by the geese. Similar results have been found on the Hudson Bay salt marsh. There, the cyanobacteria occurred mainly on bare ground and the larger nitrogen fixation in grazed areas was attributed to the presence of more bare ground (Bazely & Jefferies 1989). In our study area, the cyanobacteria were attached to the moss plants and their presence varied among moss species (Solheim et al. 1996).

Geese were not the only herbivores present in our study area. Svalbard reindeer *Rangifer tarandus platyrhynchus* also visited the study area. However, there was little harvestable vegetation left for them after the geese had grazed the area because the geese were very efficient in removing a substantial part of the annual production. The reindeer focused more on eating goose droppings (van der Wal & Loonen 1998) and probably had a minor impact on our study site, which disappears under a thick snow carpet in winter.

In conclusion, although there was no evidence that the vegetation was destroyed by the increasing number of barnacle geese, the structure of the vegetation was clearly affected by grazing. This might have an effect on breeding waders, which rely on tussocks as safe nest sites. In addition, plants which depend largely on flowering (for example *Saxifraga cernua*) were less abundant in

grazed vegetation. However, these effects cannot be seen as threats to the arctic environment. Though this study was based on two sites only, the results suggest a prudent approach before translating the habitat destruction observed in the Hudson Bay lowlands to a universal problem caused by increasing goose populations.

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

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

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Introduction

The idea that increases in animal populations are accompanied by check-and-balance mechanisms such as increased mortality, reduced production, emigration, or a combination of these, is now firmly entrenched as one of the key concepts in ecological theory (Sinclair 1989). The application of this concept of density dependence has practical implications for the management of goose populations now recovering from excessive mortality in the past as a result of hunting pressure and loss of foraging habitat. This is more fully discussed elsewhere (Ebbinge 1991; Black 1998, this volume; Loonen et al. 1998, this volume). Whether or not the population increase calls for active intervention by man is an issue that has attained prominence, not on account of the increasing conflicts with agricultural interests in the wintering and staging grounds, but more especially

due to the large scale destruction of feeding habitat on the northern tundras by the geese themselves. This is a negative impact of the recovery of goose populations which the conservation movement worked so hard to achieve. The impact has been extensively documented for the lesser snow goose *Anser caerulescens caerulescens* at various localities in Arctic Canada (see review by Batt 1997) and has led to renewed interest on the stability of the interaction between geese and their food plants on the breeding grounds elsewhere. As a contribution to this debate, we here present census data covering the establishment and stabilisation of a barnacle goose *Branta leucopsis* summer population in a small but discrete coastal area in western Spitsbergen. Fates of marked individuals identified on catching expeditions in the study area in years 1977, 1981, 1986, 1989 and 1995 help narrow the search for factors responsible for demographic change.

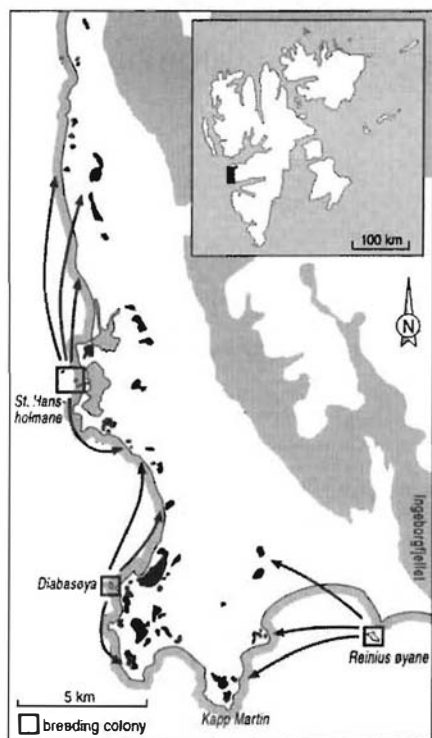


Fig. 1. Map of the Nordenskiöldkysten coastal plain study area bounded on the west by the ocean and to the east by steep mountains. Dispersal pattern of marked parents originating from the three nesting colonies (from Prop *et al.* 1980) define the counting sectors. Note the diffuse pattern of freshwater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

Study area

The coastal plain extending 40 km from Isfjorden in the north to Bellsund in the south on the western shoreline of Spitsbergen is generally known as Nordenskiöldkysten (Fig. 1). Due to relative ease of access, this area is one of the best explored parts of the archipelago. To the north, the Isfjord radio station at Kapp Linné is manned year-round by a small crew, the only locality nowadays permanently inhabited along this coast. In the past, fur trapping was an important activity here, but with the closure of the polar bear hunt between 1970 and 1973 this activity has virtually ceased and the string of huts has since fallen into disrepair. In the early years of the century, mainly between 1908 and 1926, there was a flurry of geological exploration and tentative mining at the foot of Ingeborgfjellet and on one of the Reiniusøyane at

the southern end of the area, and several cabins have survived (Hjelle 1993). Over the past twenty years, there has been very little human activity in summer aside from small field parties engaged in geological or biological survey and research and only occasional visits from small vessels (up to 1977 sealers).

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

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

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



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

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

of the Isfjord radio station and hatched their eggs successfully, surrounded by the many eider ducks that have nested in the vicinity since at least the 1950s. Norderhaug (1970) observed that island nesting was a relatively late development in the archipelago. In the 1950s and 1960s more birds were found on the offshore islands than on the traditionally used hillside sites further into the fjords.

History of the barnacle goose on Nordenskiöldkysten

Løvenskiöld (1964) reviews the early records and relates that before 1964 there was no proof of nesting on Nordenskiöldkysten. The oldest nesting colony established on this coast was first reported in 1964 when several barnacle goose families were observed close to St. Hansholmane. Breeding at Diabas was confirmed in 1968 when three nests were reported. Prestrud et al. (1989) presume that nesting at Reiniusøyane commenced at about the same time as well (1965), but the first documented count is from 1975 (Ebbinge & Ebbinge-Dallmeijer 1976). An early foot survey in June/July of 1964 attests to the fact that no barnacle geese had yet colonised on Nordenskiöldkysten (Norderhaug et al. 1965). More recently, a few pairs have nested on rocks off Båtodden (from 1975 on) and since 1996 several pairs have nested near the buildings

Survey methods

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

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

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

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

After the bulk of the geese had departed, intensive work was carried out at the Diabas colony to provide a check on the effectiveness of a single nest estimate of the breeding population. From continuous observations from a tower on the mainland tundra opposite the island, the number of nests initiated was known exactly and could be compared to the total nests counted during inventory visits to the island later in the season. Although a substantial proportion of nests abandoned at an early stage were in fact missed during the island inventories, the overall recording

covered on average 90% of all nests known to have been initiated. The effectiveness of the island survey varied somewhat from year to year depending on the numbers of pairs that had abandoned their nests early and on weather conditions that season. Counts on the island in relation to the total nest count from the continuous tower watches resulted in recovery of 91% (1979), 92.5% (1980) and 85% (1981 the year with a high rate of abandonment) of the total nests initiated that season. It can be concluded that a single nest inventory undertaken by experienced observers late in the season is unlikely to underestimate the number of nests initiated that season by more than 10%.

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

Results

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

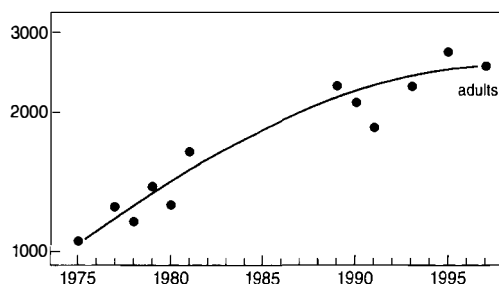


Fig. 3. Increase in numbers of barnacle geese counted along Nordenskiöldkysten during the moult, semi-logarithmic plot (ceiling value calculated by logistic growth approximation).

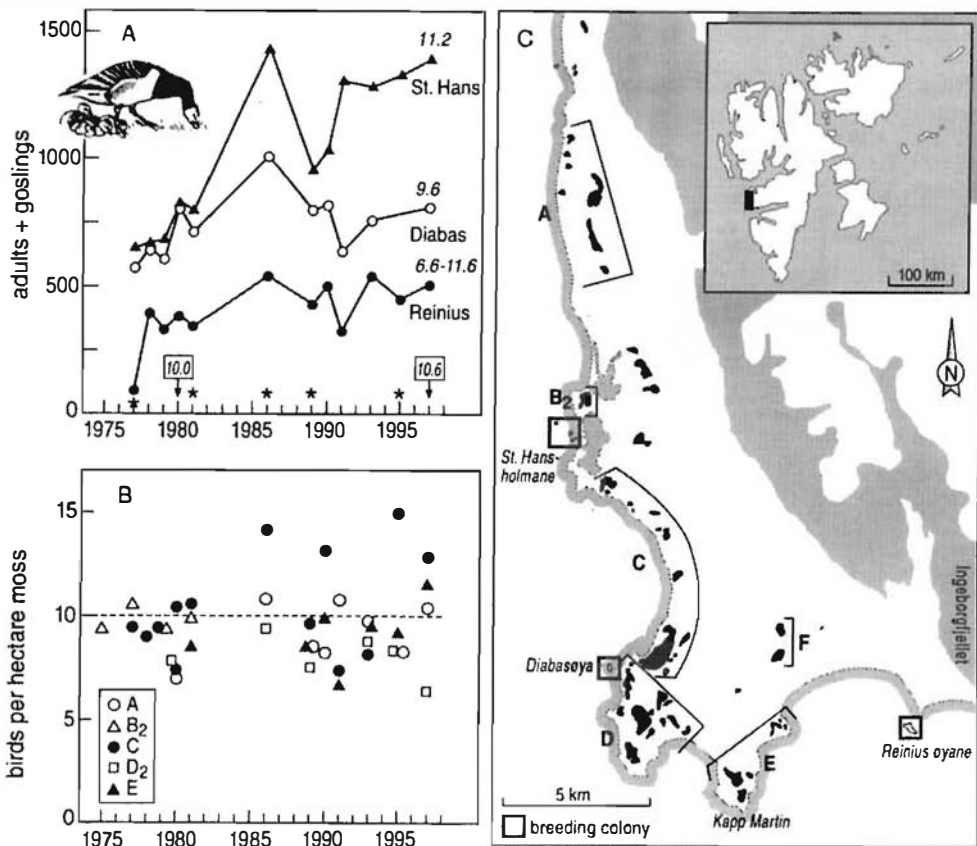


Fig. 4. Totals of adult and gosling barnacle geese (A) counted during moult per sector assigned to each colony according to Fig. 1. Note the plateau since 1986. (B) shows densities (geese per hectare suitable moss vegetation as ascertained by Prop et al. 1984) for selected tundra lake configurations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

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

have the counts of 1986 been exceeded in the six census years thereafter.

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

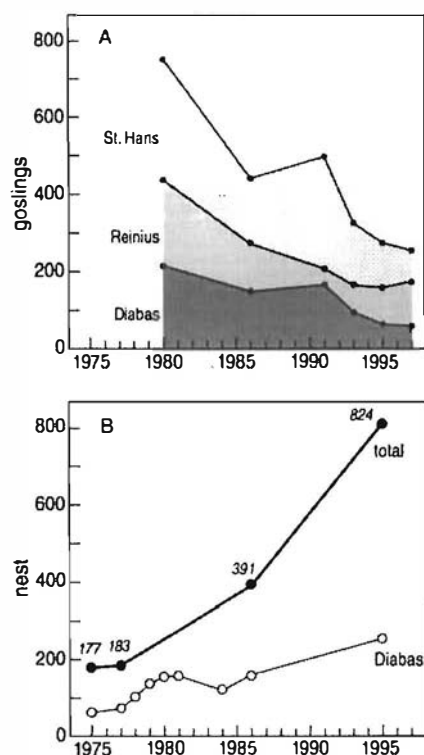


Fig. 5. Gosling production (A) and nest counts (B) for Nordenskiöldkysten barnacle geese. It will be noted that the Diabas colony was counted in more years than the others.

produced from a minimum of 177 nests (see Owen *et al.* 1978). The years 1979 and 1981 were also seasons of late snowmelt and low production (Prop

et al. 1984) and are therefore not representative for reproductive potential at that demographic stage.

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

Gosling survival to the wintering grounds in

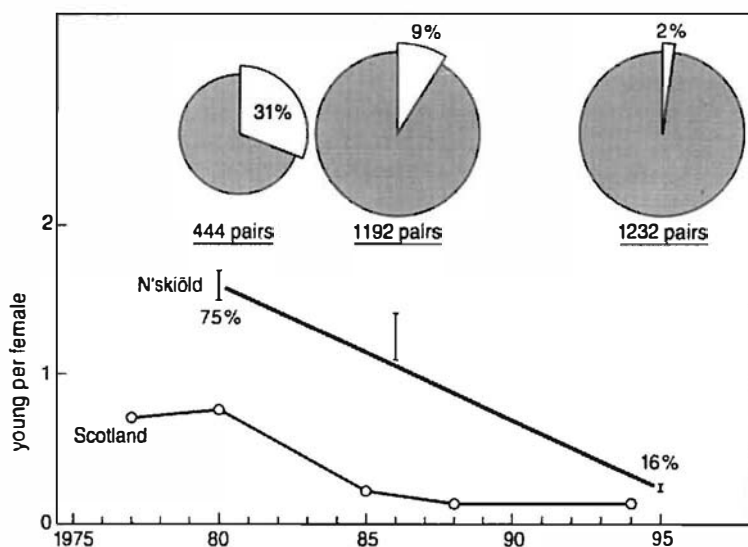


Fig. 6. Decline in productivity (goslings per female 2 years or older) of Nordenskiöldkysten barnacle geese determined during moult, compared with the same statistic upon arrival in Scotland (below) for the Svalbard population as a whole (from Black, Pettifor & Owen unpubl.). The pie diagrams present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

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

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

* not ringed on Nordenskiöld kysten.

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

Discussion

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

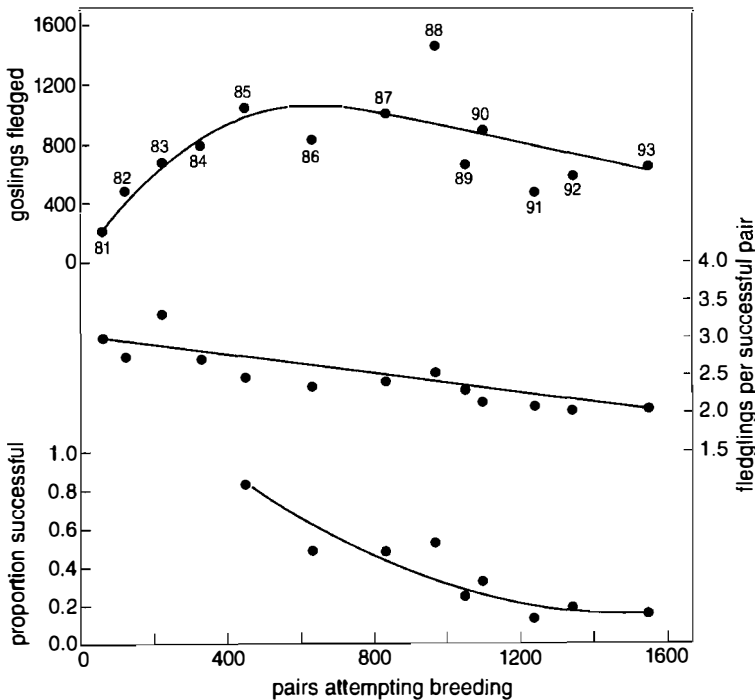


Fig. 7. Density effects in breeding output of the barnacle goose at the Laus Holmar site (Gotland, Sweden, colonised 1971) studied since 1981 by Larsson & Forslund (1994). The production of fledging geese (absolute numbers) peaks at intermediate colony size (upper curve) reflecting a steady decline in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

wintering grounds in autumn over the years 1973–1983 in relation to the number of potential breeders for the Svalbard population as a whole. He speculated that severe density-dependence was implicated. In the data set Owen presented, production peaked in the years 1976, 1978 and 1980 and was (in absolute terms) less than half of this level in the four later years. The Nordenskiöldkysten census conforms to this pattern and argues for accepting the reality of density dependence coming into action in recent years.

The analogy with the detailed demographic study of the barnacle goose population, which established naturally off the Swedish Baltic islands Gotland and Öland outside the traditional arctic breeding zone, is a close one. Larsson & Forslund (1994) followed this population since the early 1980s and, as in the Spitsbergen studies, the absolute number of goslings fledged declined as the local population increased, peaking at intermediate levels (see Fig. 7). Larsson & Forslund showed that this declining output was largely a result of a drastic decline in the proportion of pairs that laid eggs and eventually raised at least one gosling. This fall in successful parenthood was not explained by declines in clutch size or hatching success, thus implicating difficulties in the gosling phase. Larsson & Forslund emphasise that, even on the small geographic scale of their study area, large differences in output per colony were found; they further point to competitive interactions on the brood-raising areas as the density dependent agent. Although predation by gulls is the main proximate loss factor, Larsson & Forslund speculate that much of this loss is an indirect outcome of competition for food, causing goslings to be vulnerable to predation.

In our study area we have compiled detailed information on when losses in reproduction occurred for the years 1978 through 1981 (Prop *et al.* 1984), when gosling production peaked. At that time the major year-to-year fluctuations resulted from losses during the island phase, and one fourth of the goslings were lost during the brood-raising phase on the mainland tundra. From the nest counts in recent years, it can be concluded that (1) the number of pairs initiating breeding on Nordenskiöldkysten is still increasing, and (2) the low output in goslings observed during the moult census must be due to massive losses on the breeding islets or shortly after breeding when the families swim to the mainland tundra lakes where the broods are raised. The entire area is patrolled

regularly by arctic foxes *Alopex lagopus*, and glaucous gulls are present at all nesting sites so that any relaxation of parental vigilance is immediately punished. As foxes compress the brood raising areas at the Ny-Ålesund colony with a consequent decline in growth rate and survival of goslings (Loonen *et al.* 1998, this volume), it seems justifiable to infer a similar scenario on Nordenskiöldkysten. This is supported by observations from 1989 when nest success of the St. Hansholmane colony was as high as 73% (Prop & de Vries 1993) similar to values in favourable seasons (1978, 1980) in the early years at the Diabas colony. In 1989 most of the goslings reached the mainland tundra safely, but attempts to locate the family flocks only two weeks later failed indicating that most of the goslings had died in the meantime. Clarification of the causation of increased losses at the current high breeding population must await detailed field investigation, a priority item in relation to the general theoretical interest relating to the mechanisms of density-dependent population limitation (Newton 1998).

That the brood-raising areas are used to capacity is suggested by the constant density computed for the total numbers of geese using the various sectors of the coast since 1986 (as was shown in Fig. 4). We regard this density figure of 100 geese per 10 hectare as an empirical approximation of the ceiling value since the most heavily used portions of the study area already fell within this range twenty years ago (see Fig. 4B). In the original tabulation covering the years 1977–1981, Prop *et al.* (1984) showed that two tundra-lake zones B and C (Fig. 4C) had already attained the ceiling level of ca. 100 geese/10 ha graminoid vegetation, whereas the zone A to the north and D, E and F to the south experienced peak numbers in the region of 60–85/10 ha. Since that time the zone A has reached the 100 mark in four of the six census years and can thus be considered 'full'. Both sectors D and E have reached this benchmark once (in 1986 and 1997 respectively). Sector F (Eungane) is, in relation to the vegetated area, still underused to the same extent (64 versus 61 birds/10 ha). As was discussed by Prop *et al.* (1984), the relatively isolated position of this complex and the late date of ice-melt may be responsible. The Eungane system (identified in Fig. 4) is also close to a traditional denning site of the arctic fox, and foxes have been observed hunting along the lake margins every year. That disturbance by predators inhibits utilisation during the flightless period is

Table 2. Shoot density of food plants on vegetation transects near Kapp Martin sampled over an interval of approximately ten years. Data refer to mean density of shoots in plots of 400 cm² (sample size indicated) as determined in earlier year (First, 1978 or 1980 as shown) and later (either 1988 or 1989).

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

* V = Vinkelvatnet, F = Fjörängen.

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

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

The constancy of goose grazing pressures argues against deleterious impacts of goose grazing on the vegetation when viewed over a twenty-year period on individual lake margins. This is particularly true in the brood-raising phase when the geese flocks are highly concentrated.

Vegetation data, collected at an interval of a decade from transects at sites intensively grazed by barnacle geese, showed no change in density of the main food plants (Table 2). In both *Dupontia* transects, however, the moss carpet had been damaged locally (10% of the plots) by geese extracting tufts of moss in search of basal stems of their food plants. Clearly, monitoring of the vegetation will have to continue, and we hope to sample other transects from the early years in order to extend the sample.

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

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Movement of barnacle geese between colonies in Svalbard and the colonisation process

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Movements of individually ringed barnacle geese *Branta leucopsis* were recorded in Svalbard between 1962 and 1996. Detecting movements depended on the frequency of visits to the breeding grounds; thus there was a lag of 1–19 years. Of 4,339 opportunities to detect whether 2,207 birds had changed sites or not, only 213 movements occurred, indicating a high degree of site fidelity in these birds. The amount of movement (or site fidelity) varied among colonies, ranging between 3 and 45%. Emigration versus immigration also varied among colonies; more birds apparently immigrated to older colonies. Although both sexes showed a high degree of site fidelity, males were more likely to change sites than females. Although some birds of all ages changed sites, most movements were by younger birds. However, the majority of young birds did not change sites. Most colonisations were made by young geese from the largest and best studied area, Nordenskiöldkysten. Evidence suggests that geese moved to new sites together as a group or within the same period of time.

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Introduction

Describing the amount of movement between sites is a key component in the study of avian population dynamics, yet it is often most difficult to measure, requiring details of marked individuals that are tracked over time and space (Clobert & Lebreton 1991). In geese, it is believed that site use on the breeding grounds is influenced by the female's propensity to return to the area in which she was reared and the males attachment to particular females (Cooke et al. 1975; Cooke et al. 1983; Cooke et al. 1995). The mechanism behind the establishment of new sites, on the other hand, is poorly understood. The female philopatry and mate choice mechanism must not be operative when individuals venture out and establish new colonies in previously unexperienced sites.

Moving away from familiar sites to unfamiliar sites may be a risky strategy since most dispersers may not find a suitable area for settling or may end up in an area that is already occupied, thus beginning at a competitive disadvantage. For colonisation to succeed, it must result in a long-lasting population independent from additional

immigration. Several studies stress that the majority of movements between sites are by young birds, probably before they pair and have established routines within sites (Newton & Marquis 1982; Harris 1984; Lessells 1985; Brooke 1990).

From a low of 300 individuals in 1948, the Svalbard barnacle goose *Branta leucopsis* population responded to a series of conservation and management initiatives in the wintering and breeding grounds (Owen & Norderhaug 1977). In the 1990s the population reached unprecedented levels (23,000 individuals in 1996). The geese spread to new wintering areas on the Solway Firth in northern Britain and to new staging areas in Norway (Owen et al. 1987; Black et al. 1991; Prop et al. 1998). The number of colonies in Svalbard has also increased to more than 35 (Prestrud et al. 1989; Mehlum 1998, this volume). This means that a proportion of the population were 'pioneers' that colonised new sites throughout their range.

As a result of the increase in numbers, we have recorded changes in several demographic parameters, including an increased age of first breeding, an increase in the non-breeder contingent, a decline in gosling growth rate, decline in final body size, decline in many reproductive par-

ameters, and an increase in gosling and adult mortality during autumn migration (Prop et al. 1984; Owen & Black 1989a, 1991a; Loonen et al. 1997; Black et al. 1998, this volume). We believe that at some colonies these changes are directly related to a decline in food availability either through a negative response by the vegetation to intensive goose grazing (*sensu* Williams et al. 1993) or through reduced access to food due to increased competition (Prop et al. 1984; Owen & Black 1989a; Drent et al. 1998, this volume; Loonen et al. 1997, 1998, this volume). However, the population continues to rise in a stepwise fashion (Black 1998). The primary working hypothesis for the increase is the establishment of additional colonies that are not limited by density related processes (Black 1998, this volume).

I document the amount of interchange between the well-established colonies in Svalbard and describe a likely mechanism behind new colony development. To better understand the nature of movement between sites and pioneering for new sites, I was particularly interested in the following three questions: (1) Do net emigration and immigration rates vary between colonies? (2) Which individuals are the explorers and at what age do birds move between sites? and (3) What is the likely process behind new colony establishment and how many birds are involved?

Background and methods

Study sites

Nineteen regions with nesting colonies were visited between 1 and 12 times, and two were visited regularly, Nordenskiöldkysten from 1977 to 1995 and Kongsfjorden from 1989 to 1995 (Fig. 1). Most colonies in Svalbard are on small islands but they are also found on cliffs and rock skerries (Prestrud et al. 1989). We assume that colony age, as calculated from the discovery date, provides a useful variable to reflect the link between bird numbers and the quantity of food available to the geese. Although small numbers of geese may have used some of the sites for centuries before their discovery, the discovery dates indicate a relative

colony age that is closely correlated with bird density in each area (Prestrud et al. 1989).

Movements

Records of movements between sites were based on 16 catching expeditions, 5 multi-colony surveys and opportunistic observations in Svalbard between 1962 and 1996. Geese were fitted with individually engraved plastic tarsal bands (Owen et al. 1978). Sightings were restricted to the months of June through mid-August when geese were associated to particular colonies and/or their adjacent brood-rearing and moulting areas. In this paper, site fidelity refers to birds returning to the same breeding area rather than to a particular location within the area. Descriptions of such breeding areas have been made by previous authors (Owen et al. 1978; Prokosch 1984; and Prop et al. 1984).

Except where within-season movements are concerned, the location of the first resighting was used. The probability of movement and site-faithful events was calculated according to the total number of opportunities to detect such events. One encounter-year was equivalent to one opportunity to recover a bird (i.e. catch, sighting or ring found/dead) beyond the initial sighting in Svalbard in a previous year.

To determine relative rates of movement for different colonies, I compared the probability of movements and non-movements to total encounter-years. To assess net emigration/immigration rates, I compared movements to and away from each site. These values provide only minimum rates of movement since detection was obviously related to frequency and location of our expeditions.

To further elucidate the nature of pioneer types (i.e. those that moved to new sites), I described the characteristics of 11 individuals involved in multiple movements. The characteristics and origin of 24 founder individuals were obtained from 9 newly established colonies. Age estimates were minimum ages, as some birds were captured as adults. By examining the dates, origins and destinations of movements it was possible to identify the number of birds that had moved from one colony to another in the same year.

I considered the latitude of sites because birds may be more likely to know about southerly



Fig. 1. Study colonies and brood rearing areas on Svalbard, Norway. Colony/brood rearing area codes, from south to north: Dunøyane, Isøyane, Tusenøyane, Eholmen, Mariaholmen/Akseloya, Reindalen, Reiniusøyane, Diabasøya, St. Hansholmane, Daudmannsodden, Erdmannflya, Bohemanflya, Gåsøyane/Gipsdalen, Sassendalen, Hermansenøya, Forlandsøyane/Prins Karls Forland, Kongsfjorden/Ny-Ålesund, Kapp Mitra, Moseøya/Danskøya.

colonies since they passed them on migration. Similarly, colony age was considered because birds may know the whereabouts of older colonies, i.e. have had more opportunity to have discovered them. Records from the seabird cliffs were excluded from this analysis, i.e. within Svalbard staging areas (Prop et al. 1981, 1984; Tombre et al. 1997). Those within Svalbard staging areas can be a considerable distance from the birds' nest/brood rearing areas (unpubl. data). The term 'detection

year' refers to the year in which a movement was discovered.

Results

A total of 15,729 recoveries of 7,077 individuals were recorded among 19 colonies and/or brood

Table 1. Number of recoveries in Svalbard (caught, seen or ring recovered/dead). First record refers to first record of barnacle geese at the site. Colony/brood rearing area codes, from south to north: DUN = Dunøyane, ISO = Isøyane, TUS = Tusenøyane, EHO = Eholmen, MAR = Mariholmen/Akseløya, REIND = Reindalen, REINI = Reimusøyane, DIA = Diabasøya, STHA = St. Hansholmane, DAU = Daudmannsodden, ERD = Erdmannflya, BOH = Bohemianflya, GAS = Gåsøyane/Gipsdalen, SAS = Sassendalen, HER = Hermansenøya, FOR = Forlandsøyane/Prins Karls Forland, KON = Kongsfjorden/Ny-Ålesund, KMI = Kapp Mitra, MOS = Moseøya/Danskøya. The totals refer to individual birds that were recovered.

	DUN	ISO	TUS	EHO	MAR	REIND	REINI ^a	DIB ^a	STH ^a	DAU	ERD	BOH	GAS	SAS	HER	FOR	KON	KMI	MOS	Total
Latitude °N	77.03	77.09	78.09	77.34	77.39	77.52	77.44	77.45	77.52	78.15	78.15	78.23	78.25	78.19	78.32	78.20	78.55	79.07	79.37	
First record	1938	1938	1987	1987	1989	1954	1975	1968	1963	1970	1980	1980	1982	1963	1989	1963	1982	1984	1984	
Years with records	11	5	3	1	2	1	10	13	8	4	1	1	3	5	1	3	10	1	1	19
Total birds	560	366	7	14	14	3	1,136	1,944	1,808	346	16	160	407	117	1	87	1,130	2	17	7,077

^a = these areas were lumped together as Nordenskiöldkysten (NOR) for subsequent analyses.

rearing areas (Table 1; Fig. 2). Over 100 records were obtained in 15 of the 24 years, and over 1,000 records were achieved in four years. The majority of observations were from capturing ($n = 9,604$) and resightings live birds ($n = 6,090$), augmented with records of rings from dead birds ($n = 35$).

Within-year movements

There were 389 within-year movements, of which 387 were among the three colonies and associated brood rearing areas on Nordenskiöldkysten. These movements consisted of overland journeys between fresh water lakes at distances of between 3–15 km (see Prop et al. 1984). The majority of the movements on this coastline were probably caused by our catching activities. The coast was therefore treated as a homogeneous unit in subsequent analyses. The other two within-year movements provided some information on the potential timing and nature of movements between sites:

(1) The well-established pair, >CH & >CJ, were recorded at a nest on Isøyane (21.06.89). Forty days later they were caught 50 km north in the Diabasøya area of Nordenskiöldkysten (31.07.89). They must have flown to the new site with their old primaries because when caught they were about 15 days into their moult. They had no young with them on the wintering grounds. The site change was in the direction of the male's natal area and away from the female's; in 1986, >CH, the male, was ringed as a gosling on Nordenskiöldkysten, whereas >CJ, the female, was ringed near Isøyane.

(2) An adult male, >CHH, was captured and ringed in the Sassendalen brood rearing area (30.07.93). Five days later he was caught 20 km north at Gipsdalen (04.08.93). This journey, which occurred during the moult, probably included a 10 km swim across Sassenfjorden. This bird and his mate >CHJ, who was also caught in Sassendalen (30.07.93), subsequently used Gipsdalen in 1994.

These records indicate that birds can move between sites within a summer season. The remainder of the paper deals with between-year site changes during the nesting or moulting periods.

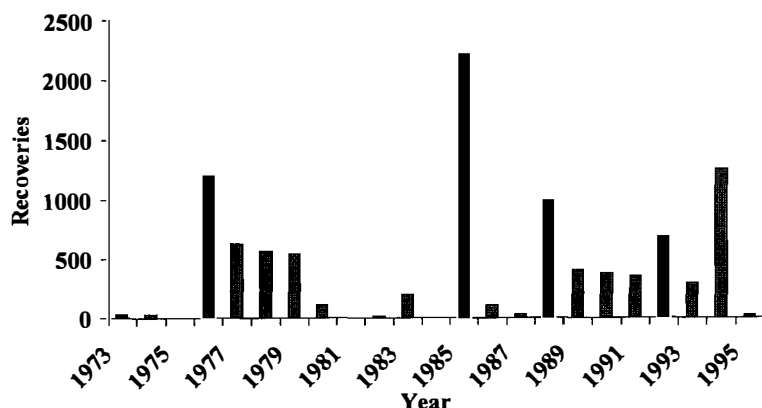


Fig. 2. Relative recovery effort during the study period; total number of records.

Between year movements and site fidelity

Excluding within year movements, 6,546 recoveries allowed 4,339 opportunities (encounter-years) to detect whether 2,207 birds had changed or remained at sites. Table 2 lists the origin and destination of 213 movements. Totals refer to individual birds that were recovered. The longest movement of 280 km was between Kongsfjorden/Ny-Ålesund (Northwest) and Tusenøyane (Southeast). This change of site was completed by a female (*VYI; ringed as an adult in 1992) between 1993–1996. Three sites with most movements between them were: Nordenskiöldkysten to Forlandsøyane ($n = 21$), Nordenskiöldkysten to Dunøyane ($n = 18$), Nordenskiöldkysten to Daudmannsodden ($n = 14$) and Daudmannsodden to Nordenskiöldkysten ($n = 14$).

The proportion of birds that changed sites (compared to total encounter-years) varied between 3 and 45% among colonies (mean 5%; Table 3). This means that 55–97% of the birds were faithful to sites during the study period; the overall rate being 95%. The two youngest colonies (Gåsøyane/Gipsdalen and Kongsfjorden/Ny-Ålesund) had high site fidelity rates (over 92%), as did Nordenskiöldkysten. The lowest site fidelity rates (52–55%) were from Isøyane and Daudmannsodden. Comparing all colonies in Table 3, site fidelity (and movement rate) was not correlated with colony latitude, colony age or net immigration/emigration.

The ratio of immigration to emigration ranged from 0.4 (Nordenskiöldkysten) to 3.0 (Sassendalen), the second value indicating 3 movements in, to one outward movement. More birds

immigrated to older colonies than younger colonies (Mann-Whitney U-test comparing the four oldest with the four youngest colonies = 2, $P = 0.057$, 1-tailed test). The in/out ratio was not related to colony latitude.

Bird sex and age

Males were more likely to move than females; 6.5% of males and 3.3% of females (males: 133 movements, 1906 site faithful events; females: 74 and 2,193; Chi Square = 24.9, $df = 1$, $P < 0.001$). This means that females were more site faithful than males. The detection lag for movements ranged between 1 and 19 years (mean 4.4, SE 0.2, $n = 213$; Fig. 3A). Therefore, I present minimum and maximum values for calculating the age at which birds changed sites. Using a minimum estimate causes difficulties when referring to the gosling year. It is unlikely that goslings change sites until the following yearling year. Similarly, the majority of adults may actually change sites in years subsequent to the estimated maximum age. Providing a range of ages enables a more realistic assessment of when movements occurred.

With both methods it was clear that birds changed sites throughout their lifetimes. Using the most conservative method, 6% of the site changes involved birds aged 5 or more years; the mean age was between 2.2 (minimum age, SD 2.0) and 6.1 (maximum age, SD 3.7). Movements and site faithful events varied significantly among age classes, comparing movements and site faithful events for minimum ages of 1–3, 4–6, 7–11 years (Chi Square 211.4, $df = 2$, $P < 0.001$) and maxi-

Table 2. Origin and destination of 213 movements between sites. Listed from south to north.

Origin	Destination	Number of movements
Dunøyane	Isøyane	9
	Nordenskiöldkysten	13
	Forlandsøyane	2
	(Prins Karls Forland)	
Isøyane	Ny-Ålesund (Kongsfjorden)	1
	Dunøyane	3
	Nordenskiöldkysten	7
	Ny-Ålesund (Kongsfjorden)	1
Reindalen	Nordenskiöldkysten	1
Nordenskiöldkysten	Dunøyane	18
	Isøyane	7
	Tusenøyane	1
	Mariaholmen/Akseløya	11
	Eholmen	9
	Forlandsøyane	21
	(Prins Karls Forland)	
	Daudmannsodden	14
	Sassendalen	5
	Bohemanflya	3
	Hermansenøya	1
	Kapp Mitra	2
	Ny-Ålesund (Kongsfjorden)	9
	Moseøya (near Danskøya)	9
Daudmannsodden	Dunøyane	3
	Nordenskiöldkysten	14
	Forlandsøyane	3
	(Prins Karls Forland)	
	Ny-Ålesund (Kongsfjorden)	2
Bohemanflya	Nordenskiöldkysten	1
	Sassendalen	1
Sassendalen	Gåsøyane/Gipsdalen	4
Gåsøyane/Gipsdalen	Eholmen	6
	Sassendalen	1
	Ny-Ålesund (Kongsfjorden)	1
	Nordenskiöldkysten	1
Forlandsøyane	Daudmannsodden	3
(Prins Karls Forland)	Dunøyane	3
Ny-Ålesund (Kongsfjorden)	Tusenøyane	1
	Mariaholmen/Akseløya	1
	Eholmen	1
	Nordenskiöldkysten	10
	Gåsøyane/Gipsdalen	10

num ages of 1–3, 4–6, 7–11 and 12–22 years (Chi Square 28.9, df = 3, $P < 0.001$). Examination of the contingency tables indicated that while the vast majority of birds were site faithful at all ages, younger birds were less site faithful and moved

more often than expected, and older birds were more site faithful and moved less than expected.

Using minimum ages, the probability of movement events (to total encounter-years) was about 24% in young birds (0–3 years), 1% in middle-

Table 3. Number of recoveries in Svalbard for 2,207 birds that were seen beyond the initial year (caught, seen or ring recovered/dead). Colony/brood rearing area codes, from south to north: DUN = Dunøya, ISO = Isøyane, MAR = Martholmen/Akseøya, REIND = Reindalen, NOR = Nordenskiöldkysten, DAU = Daudmannsodden, BOH = Bohemianfya, GAS = Gåsøyane/Gipsdalen, SAS = Sassendalen, FOR = Forlandsøyane/Prins Karls Forland, and KON = Kongsfjorden/Ny-Ålesund. The totals refer to individual birds that were recovered.

	DUN	ISO	MAR	REIND	NOR	DAU	BOH	GAS	SAS	FOR	KON	Total
Encounter years	107	22	1	1	3,227	49	2	102	19	8	801	4,339
Emigrated	25	11	0	1	110	22	2	8	4	4	26	213
% Site fidelity	76.6	52.4	-	-	96.6	55.1	-	92.2	-	-	96.8	95.1
Immigrated	27	16	12	0	47	17	3	14	12	26	14	213 ^a
Net movement	Immi	Immi	-	-	Emig	Emig	-	Immi	Immi	Immi	Emig	

^a = with 25 other immigration records this value amounts to 213; these included site TUS = Tusenøyane (2 immigrations), EHO = Eholmen (1), HER = Hermansenøya (1), KMI = Kapp Mitra (2), MOS = Moseøya/Danskøya (9). See Table 5 concerning establishment of new colonies.

aged classes (4–6 years), and 2% in the older birds (7–11 years; Fig 3B). Using maximum ages, the proportion of birds that changed sites varied from 6% in young birds (1–3 years), to 4% (4–6 years), to 7% (7–11 years), and increased to 13% in the oldest birds (12–20 years; Fig 3C).

There was no difference in the age at which males and females changed sites, for example, when comparing movements with minimum ages 0, 1, 2, 3+ (Chi Square 6.0, df = 3, NS).

Characteristics of birds with multiple movements: case studies

Excluding individuals with only a single encounter-year, 4,184 recoveries allowed 3,158 opportunities (encounter-years) to detect whether 1,026 birds had changed or remained at sites in more than one year.

Most birds that moved were detected to have moved only once (193 of 204 birds). Eleven individuals moved more than once (Table 4). In nine of these cases the second movement was back to the original location, 8 returning to Nordenskiöldkysten and the other to Isøyane. In two cases, a male and female of two known pairs completed these outward and return movements. The return movements to Nordenskiöldkysten were on average two years after the initial move (range 1–3, SD 0.4). The movement back to Isøyane was after a 7–12 year period. The other cases involved one long distance move followed by a move to an adjacent colony: (1) from Ny-Ålesund down to Gipsdalen, then to Sassendalen in the next year and (2) from Forlandsøyane to Nordenskiöldkysten, then to Daudmannsodden after 3–6 years.

These pioneers consisted of 4 females and 7 males. Their average minimum age at the first move was between 2.1 (minimum: range 0–6 years, SD = 1.5) and 4.7 years (maximum: range 2–9 years, SD 2.2). The average age at the second move was between 5.0 (minimum: range 2–9 years, SD 2.4) and 7.4 years (maximum: range 3–17 years, SD 4.0).

Characteristics of colony founders: case studies

The identity of 24 individuals was recorded in the

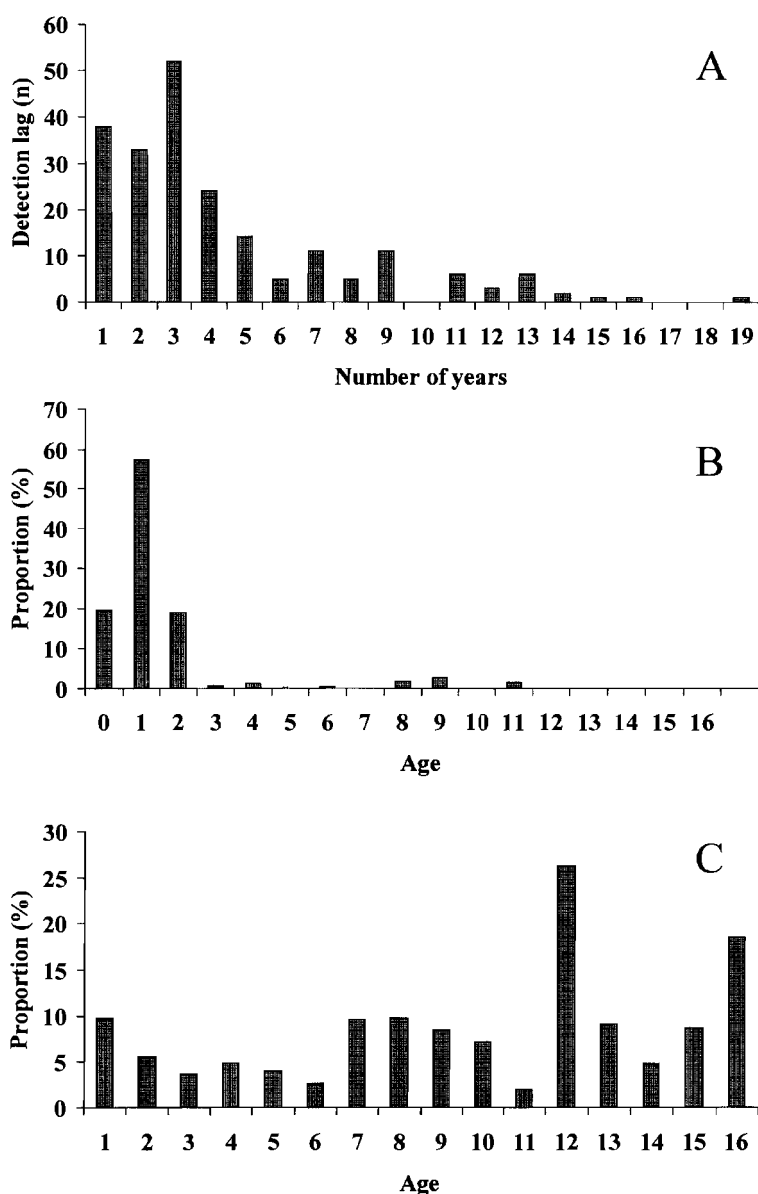


Fig. 3. Estimated age at which birds changed sites: A. Detection lag in years; B. proportion of movements – minimum age; C. proportion of movements – maximum age.

same year or soon after colony discovery (Table 5). Twenty-two of the founders originated from Nordenskiöldkysten. The other 2 came from Dunøyane and Daudmannsodden.

These founders consisted of 7 females and 17 males. Their average minimum age was 1.3 (range 0–4 years, $SD = 1.0$) and the maximum age was 5.1 (range 1–15 years, $SD = 3.2$) in the detection year.

Group movements: case studies

To detect potential group sizes involved in movements, I checked the 213 movements for birds that in the same detection year moved from and returned to the same locations. Potential group size ranged between 1 and 16 individuals; 44% of the movements were in potential groups of 5 or

Table 4. Characteristics of 11 barnacle geese that changed sites more than once; both moves are listed in sequence. Note: the first two and second two birds are male-female pair members. M = minimum age (years); R = real age (years).

Moved to	Moved from	Bird sex	Min Yr	Min Age	Max Yr	Max Age	Age type
Daudmannsodden	Nordenskiöldkysten	*DTA M	77	2	79	4	M
Nordenskiöldkysten	Daudmannsodden		79	4	81	6	
Daudmannsodden	Nordenskiöldkysten	*DVD F	77	2	79	4	M
Nordenskiöldkysten	Daudmannsodden		79	4	81	6	
Daudmannsodden	Nordenskiöldkysten	*HAY M	77	2	79	4	M
Nordenskiöldkysten	Daudmannsodden		79	4	81	6	
Daudmannsodden	Nordenskiöldkysten	*HDA F	77	2	79	4	M
Nordenskiöldkysten	Daudmannsodden		79	4	81	6	
Daudmannsodden	Nordenskiöldkysten	*DDG M	77	2	79	4	M
Nordenskiöldkysten	Daudmannsodden		79	4	81	6	
Daudmannsodden	Nordenskiöldkysten	*DNB M	77	1	79	3	R
Nordenskiöldkysten	Daudmannsodden		79	3	81	5	
Forlandsøyane	Nordenskiöldkysten	*CRS M	81	6	84	9	M
Nordenskiöldkysten	Forlandsøyane		84	9	86	11	
Ny-Ålesund	Nordenskiöldkysten	*MU F	86	0	88	2	R
Nordenskiöldkysten	Ny-Ålesund		86	2	89	3	
Nordenskiöldkysten	Isøyane	*HFV M	73	1	77	5	M
Isøyane	Nordenskiöldkysten		80	9	89	17	
Gipsdalen	Ny-Ålesund	*ERK F	91	2	93	4	M
Sassendalen	Gipsdalen		93	4	94	5	
Forlandsøyane	Nordenskiöldkysten	*DIK M	78	3	84	9	M
Daudmannsodden	Forlandsøyane		84	9	86	11	

more individuals (Fig. 4). Average potential group size was 2.7 individuals (SD 2.6). The largest potential group ($n = 16$) was from Nordenskiöldkysten to Forlandsøyane/Prins Karls Forland, detected in 1984.

The first six birds listed in Table 4, including two pairs, completed their outward movement from Nordenskiöldkysten to Daudmannsodden in the same year. Their return to Nordenskiöldkysten was also detected in the same year. The distance between these sites was between 50 and 80 km.

Just because the birds were detected at the destination in the same year does not indicate that the geese travelled together in one flock. However, further evidence for group movements may come from examining the bird-ages (i.e. cohorts) together with dates, origins and destinations. Six potential cohort movements were notable: (1) Between 1981 and 1984, 5 birds from the 1976 Nordenskiöldkysten cohort moved 75 km North-west to Forlandsøyane/Prins Karls Forland; (2) Between 1981 and 1984, 5 birds from the 1980 Nordenskiöldkysten cohort moved 225 km North-

west to Moseøya; (3) Between 1986 and 1990, 5 birds from the 1985 Dunøyane cohort moved 90 km north to Nordenskiöldkysten; (4) Between 1991 and 1993, 9 birds from the 1991 Ny-Ålesund cohort moved 115 km Southeast to Gipsdalen; (5) Between 1995 and 1996, 10 birds from the 1995 Nordenskiöldkysten cohort moved 25 km south to Mariaholmen/Akseløya; (6) Between 1995 and 1996, 8 birds from the 1995 Nordenskiöldkysten cohort moved 32 km south to Eholmane.

Discussion

The density-related processes that affect established colonies in Svalbard are thought to be competition for a limited amount of high quality food on the breeding grounds (Prop et al. 1984; Owen & Black 1989a; 1991a) and the fluctuating presence of goose predators, namely the arctic fox *Alopex lagopus* (Loonen et al. 1998, this volume).

Table 5. Characteristics of 24 pioneer barnacle geese – founders of new colonies. M = minimum age (years); R = real age (years).

New colony destination	Origin		Bird sex	Min year	Min age (yrs)	Max year	Max age (yrs)	Age type
Ny-Ålesund	Nordenskiöldkysten	*BD	F	86	1	87	2	R
Ny-Ålesund	Nordenskiöldkysten	*LTH	M	86	2	87	3	M
Ny-Ålesund	Nordenskiöldkysten	*PDJ	F	86	2	87	3	M
Ny-Ålesund	Nordenskiöldkysten	*VTN	M	86	2	87	3	M
Ny-Ålesund	Daudmannsodden	*VSY	F	86	1	87	2	M
Ny-Ålesund	Nordenskiöldkysten	*MU	F	86	0	88	2	R
Ny-Ålesund	Dunøyane	*ECC	M	86	2	88	4	M
Moseøya	Nordenskiöldkysten	\$BP	M	81	1	84	4	R
Moseøya	Nordenskiöldkysten	\$CU	M	81	1	84	4	R
Moseøya	Nordenskiöldkysten	\$YY	M	81	1	84	4	R
Moseøya	Nordenskiöldkysten	*CKC	M	77	1	84	8	R
Moseøya	Nordenskiöldkysten	*DUZ	M	80	4	84	8	R
Moseøya	Nordenskiöldkysten	*EG	F	77	0	84	7	R
Moseøya	Nordenskiöldkysten	*HDK	M	79	3	84	8	R
Moseøya	Nordenskiöldkysten	*XAV	M	81	1	84	4	R
Moseøya	Nordenskiöldkysten	*XBJ	F	81	1	84	4	R
Tusenøyane ¹	Nordenskiöldkysten	*CAS	M	77	1	91	15	R
Mariaholmen	Nordenskiöldkysten	<NA	M	86	0	89	3	R
Bohemanflya	Nordenskiöldkysten	*EPT	M	86	0	90	4	R
Bohemanflya	Nordenskiöldkysten	*EPZ	F	86	2	90	6	M
Bohemanflya	Nordenskiöldkysten	*YIZ	M	79	1	90	12	R
Hermansøyane	Nordenskiöldkysten	*FX	M	86	0	89	3	R
Kapp Mitra	Nordenskiöldkysten	\$XP	M	81	1	84	4	R
Kapp Mitra	Nordenskiöldkysten	\$YH	M	81	2	84	5	M

¹ = Meinickeøyane, Tusenøyane (J. M. Madsen pers. comm.).

On arrival to the breeding grounds, geese are presented with three options: (1) return to their traditional site where competition and/or predation risk may be high, (2) join others at another established site, or (3) attempt to establish a new site. Choosing the first option enables the birds to build on past experiences, but choosing the latter two options means that the birds will have little or no experience at the site. However, if competition at the new site is reduced, the birds may gain access to foraging and breeding areas sooner. The choice of whether to stay or to leave the traditional site should depend on the probability of surviving and breeding (Slobodchikoff & Schultz 1988) which may be influenced by the presence or absence of kin associations (Greenwood 1984).

Horn (1984) states that 'Different degrees of competition and crowding at various stages of life are important in determining the likelihood of an individual establishing itself locally versus at a distance. This in turn determines the adaptive value of dispersal.' The strength of selection that

favours dispersal will depend on the proportion of pioneers that survive and reproduce.

This paper focuses on between-year movements that were detected during periodic expeditions to Svalbard. Within-season movement between breeding and moulting sites probably occurs rarely, although we detected two such events. I show that most barnacle geese employ the 'site faithful' option (95% of 4,339 encounter-years), which probably means that most birds spend their lifetime visiting just one breeding location in Svalbard.

The ratio of immigration to emigration varied greatly between colonies. The probability of colonies receiving immigrants is apparently higher in the older colonies. Of the 213 recorded site changes, 189 (89%) were between two well-established sites. Of these, 145 (70%) were to older sites (pre-1980s) and 44 (30%) were to more recently established sites. There was no indication that the more southerly colonies, which most birds pass during migration, received more immigrants.

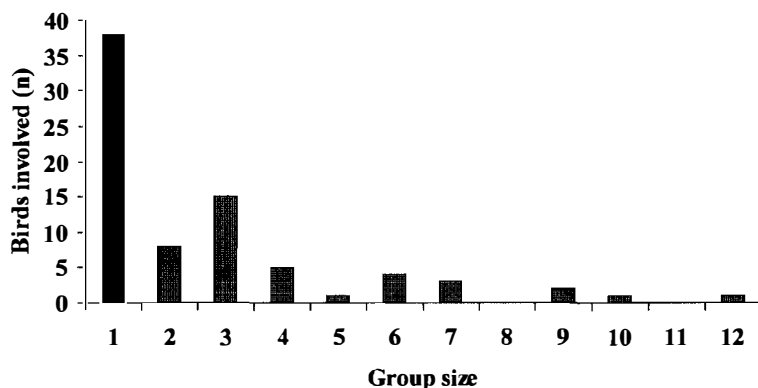


Fig. 4. Number of birds involved in movements with the same origin, destination and detection date.

These crude values on immigration/emigration rates enable a tentative formulation of ideas about the birds' behaviour in Svalbard, which can be revised when the data are considered in a more rigorous capture-recapture model that controls for temporal and spatial variation.

Evidence from birds with multiple records of site changes indicates that movements to particular sites are not always permanent. In nine of eleven cases the birds returned to their original sites after a 2–12 year period at a new site.

In two cases the outward and return movements were made by established pairs indicating that site change can be free from mate-status effects. That birds return to previously experienced sites may indicate that sampling and comparison of alternatives may occur.

The Nordenskiöldkysten birds, which were the largest sample of marked individuals and the largest concentration of geese, moved to 13 of the 16 other potential locations. It was notable that whereas, most Nordenskiöldkysten birds moved to either Forlandsøyane, Dunøyane or Daudmannsodden, they were not recorded at Gipsdalen, where a recently established flock was rapidly developing. In contrast, the birds that moved from Ny-Ålesund favoured the Gipsdalen site. This may indicate that choice of alternative sites may be influenced by cultural or learned criteria, rather than a random redistribution process.

Males changed sites more than females, regardless of age. Geese of all ages changed sites, but evidence suggests that a larger proportion of young birds may have changed sites; depending on the age estimation method employed, one in 4 or one in 17 young birds (<4 years) changed sites (Fig. 3). On examination of the frequency

distribution tables, younger birds were less site faithful and moved more than expected, while older birds were more site faithful and moved less than expected. It is clear, however, that most birds, even young birds, remained in the area in which they were initially recorded. In many cases this initial area was their natal area, and in other cases it was the site of their second summer, i.e. their yearling year.

Using a method regarding return rates to one of the colonies, Loonen et al. (1998, this volume) found that significantly fewer young birds were subsequently resighted than older birds. Evidence from the Nordenskiöldkysten indicates that fewer and fewer yearlings have returned to their natal area. This suggests that dispersal of young birds has increased with increased density and competition for food, nests and mates (Drent et al. 1998, this volume). Young, unpaired geese are at the bottom of the social hierarchy in terms of fighting and foraging skills (Lamprecht 1986; Black & Owen 1987, 1989a, b). By moving to different sites or by colonising new areas, young geese may succeed in breeding attempts sooner than by remaining in a familiar, but highly competitive situation inherent at some natal areas.

Colony establishment

I provide evidence that colony founders include young, explorative birds, predominantly males, in their second to sixth summers. Nordenskiöldkysten birds were responsible for most of the detected colonisations during the study period. This site not only had the largest concentration of

geese in Svalbard (Black 1998, this volume), but it also had the largest sample of ringed birds. These birds are characterised as large in size and capable of producing large broods (Prop et al. 1984; Owen & Black 1989a, b, 1991b; Black et al. 1998, this volume). The majority nest on islands adjacent to feeding areas (Prop et al. 1984; Prestrud et al. 1989).

Travelling in groups may make the colony establishment option more feasible because costs of predator detection are shared and food finding ability is enhanced (Pulliman & Caraco 1984). The group movement data may indicate that flocks of geese travel together to new sites and that these birds may be familiar with one another since some are from the same cohorts, i.e. reared in the same place at the same time. Coexisting with familiar neighbours may be beneficial in terms of shared vigilance, conflict situations and food finding.

Evidence from the Kongsfjorden area suggests that there is a 5–10 year lag between the discovery of a new site and successful breeding. A flock of 135 non-breeders was first discovered in 1977 (Prestrud pers. comm.). Five years passed before the first nest appeared in the area and a further five years elapsed before 15 nests were established, but thereafter the number of nests rapidly increased to 250 nests in 1996 (and 650 individuals) in the region (Loonen et al. 1998, this volume).

The lag between colony discovery, breeding attempts and subsequent successful breeding may be the result of learning about the new site. A study at the spring staging area in Helgeland has shown that birds improved their foraging performance over a three-year period, through the cumulative discovery of rich feeding patches (Prop & Black unpubl. data). It seems that each year these birds build on information gained. The foraging routes that they follow through a microhabitat and which sites they return to are influenced by previous foraging performance. They tend to return to patches and sites where they experience the highest intake rates (Prop & Black unpubl. data).

In addition to learning the location of the best foraging areas, geese in the Arctic may also need time to assess the relative predation risk of sites and microhabitats within the sites. Acquiring this knowledge may take a number of years because of the variation in arctic fox numbers and the timing of snow melt, for example the disappearance of ice bridges to islands and cliff faces.

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

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

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Introduction

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

Body size is a critical feature for geese that strive to avoid aerial attacks from predators and attempt to migrate long distances efficiently. Geese must also be able to compete with numerous flock members for forage, mates and nest sites, in addition to avoid ground dwelling predators. Whereas small body sizes may be useful in some situations, larger body size may be adaptive in others (Black et al. 1996; Choudhury et al. 1996). Several recent studies of arctic geese have found that the amount and quality of food that a gosling obtains in early life (<8 weeks) affects adult body

size (Cooch et al. 1991a; Sedinger & Flint 1991; Larsson & Forslund 1991, 1992; Sedinger et al. 1995; Loonen et al. 1997, 1998 (this volume). The argument from the lesser snow goose *Anser caerulescens caerulescens* study is that several traits, including body size, have changed over time due to the deleterious effect that overgrazing has had on the vegetation that the geese require (Cooch et al. 1991b; Cooke et al. 1995). We have yet to detect a decline in vegetation quality in our study but have begun to see signs of increased competition for a limited amount of food (Prop et al. 1984; Owen & Black 1989, 1991; Loonen 1997). In either case, goslings with limited food and suboptimal growth become small adults, while goslings reared with sufficient food become larger adults. Similar phenomena are suspected in a range of animals (Clutton-Brock 1988b), but evidence is fairly limited in vertebrates, for example final body size of young deer varies according to foraging and suckling performance (Klein 1970; Clutton-Brock et al. 1982; Albon et al. 1987).

Adult body size variation within goose popula-

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

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

Methods and procedures

The population

In the 1940s, the barnacle goose population in Svalbard declined to only 300 individuals. The population responded to a series of conservation and management initiatives in the wintering and breeding grounds with an increase of 7.8% per year since 1960 (Pettifor *et al.* 1998, this volume). In the 1990s, the population reached unprecedented levels (23,000 individuals in 1996), and the geese expanded their range in the wintering haunts on the Solway Firth, in northern Britain, and on staging areas in Norway (Owen *et al.* 1987; Black *et al.* 1991; Prop *et al.* 1998). The number of colonies in Svalbard has also increased to more than 35, mainly on the western coast of Spitsbergen between 77° and 80°N (Prestrud *et al.* 1989). The population is probably larger now than in the past (Black 1998a). As a result of the increase in numbers, we have recorded changes in several demographic parameters, including an increased age of first breeding, a large increase in the non-

breeder contingent, a decrease in many reproductive parameters, and an increase in gosling and adult mortality during autumn migration (Prop *et al.* 1984; Owen & Black 1989, 1991; Pettifor *et al.* 1998, this volume). We believe that many of these changes are directly related to a decline in food availability, either because of vegetation depletion due to intensive goose grazing (*sensu* Williams *et al.* 1993) or because of reduced access to food due to increased competition (Prop *et al.* 1984; Owen & Black 1989).

Study sites

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

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

Measurements

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

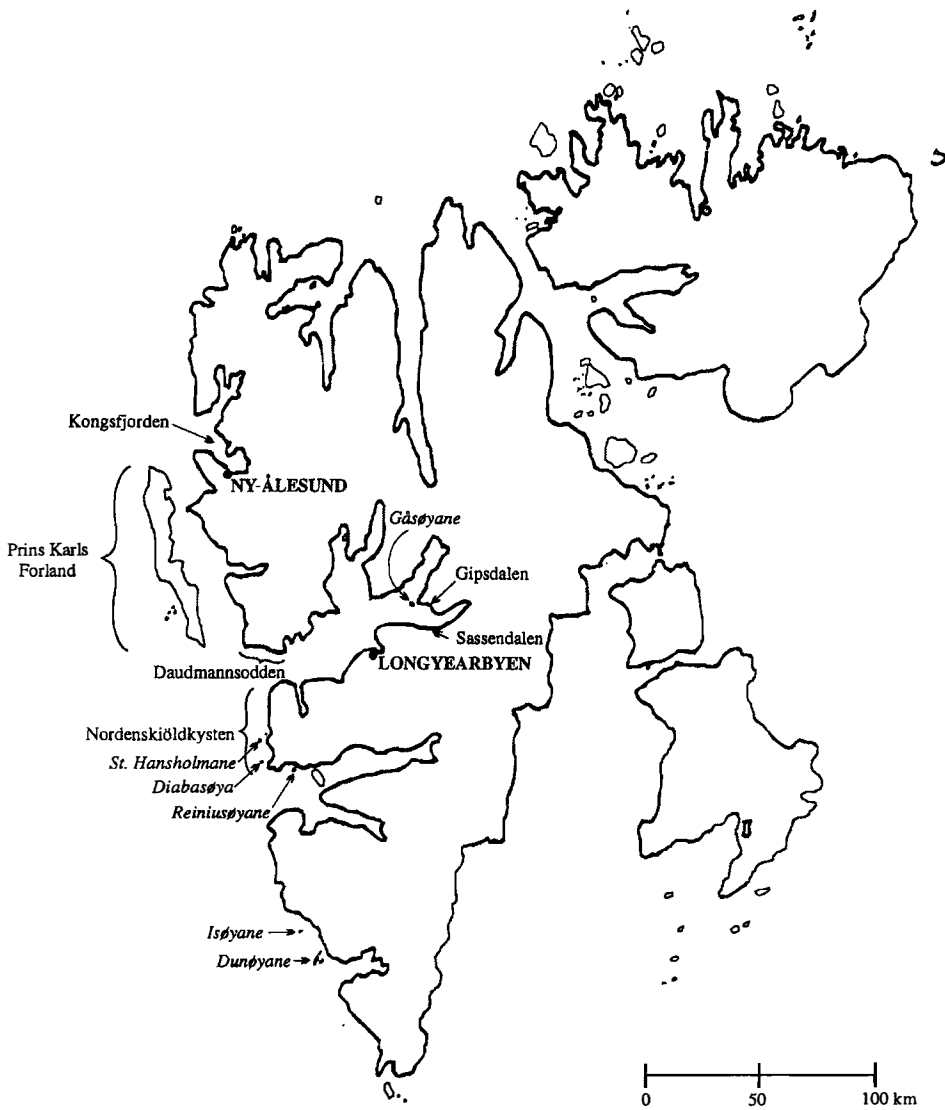


Fig. 1. Map showing the study colonies and brood rearing areas on Spitsbergen, Svalbard.

goslings is known to be more sensitive to variations in early growth conditions than skeletal characters (see for example Cooch et al. 1991b, 1996), adult body mass measured at ringing is much affected by breeding status (Owen & Ogilvie 1979; Choudhury et al. 1992). Many ringing campaigns were significantly biased with respect to breeding status. Thus, we restricted our analyses

to head and tarsus length ('tarsus bone' – Dzubin & Cooch 1992; both characters measured to the nearest 0.1 mm). We used the mean of measurements made for each individual in the sample in different years to minimise effects of measurement error. This is valid since barnacle geese do not grow significantly after the first year (Owen & Ogilvie 1979).

Statistical approach

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

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

Assigning natal colony

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

Assigning age (Cohort)

Birth-year of birds ringed as goslings and yearlings (and therefore birth-cohort) was determined precisely. Birds marked as adults were assigned a minimum age of two years (and thus a birth-cohort of year-2). The earliest age of first-breeding in barnacle geese is two years. However, there are

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

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

Results

Within-colony variation (temporal scale)

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

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

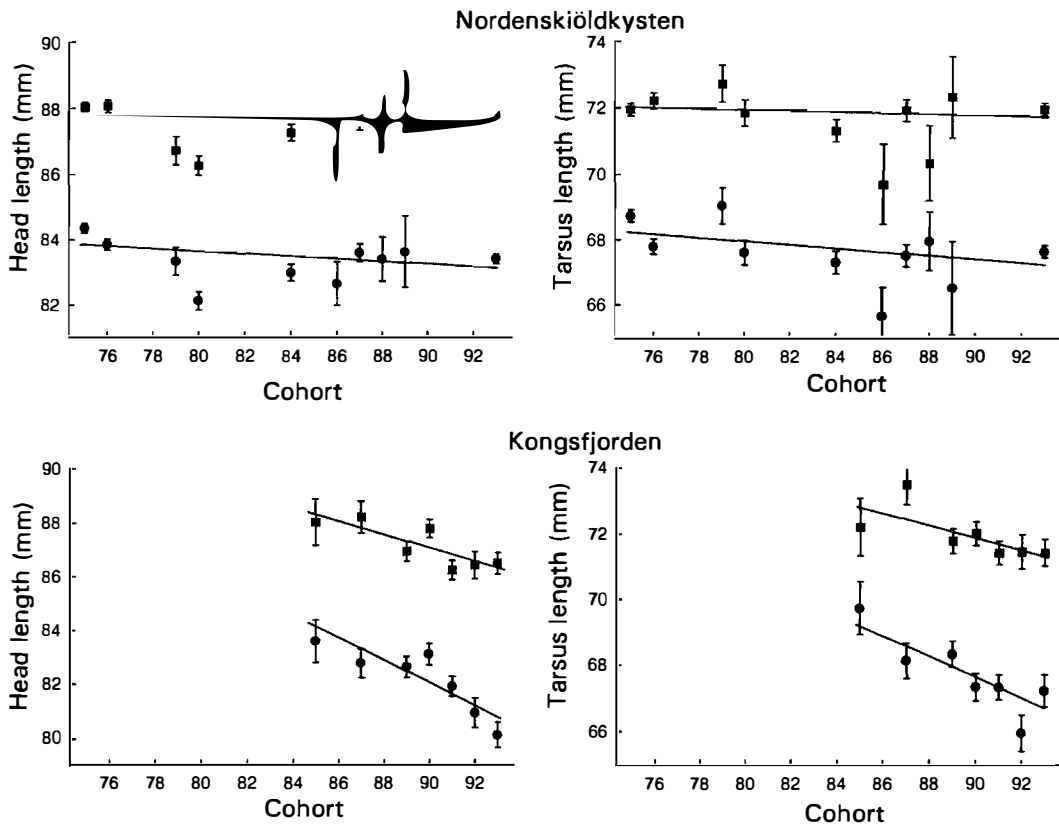


Fig. 2. Variation in head and tarsus measures over several cohorts for birds living in two localities. There was a highly significant long-term decline in head for both the Nordenskiöldkysten (ANCOVA $F_{1,2179} = 13.76$, $P < 0.001$) and Kongsfjorden colonies (ANCOVA $F_{1,635} = 34.92$, $P < 0.001$)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

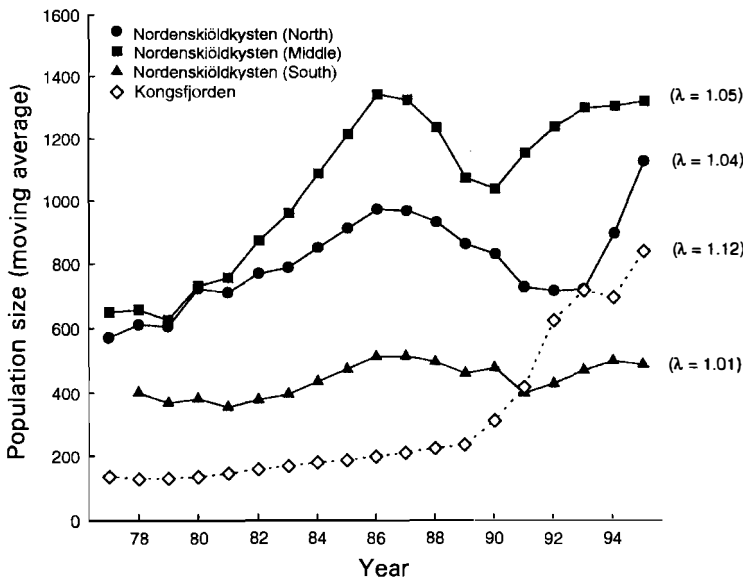


Fig. 3. Number of geese (including breeders and non-breeders) and population growth (given as λ values) for three Nordenskiöldkysten sub-colonies and the Kongsfjorden area. We calculated values for missing years using a simple linear interpolation (excluding the spurious value for the south in 1977)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

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

Between colony variation (spatial scale)

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

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

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

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

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

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

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

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

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

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

Colony	Latitude	First colony record	Female head length	Male head length	Female tarsus length	Male tarsus length	Sample sizes Male, Female
Isøyane and Dunøyane ¹	77.05°N	1938	82.00 (0.20)	86.53 (0.21)	65.51 (0.24)	70.43 (0.25)	193, 192
Nordenskiöldkysten ²	77.50°N	1969	83.60 (0.07)	87.71 (0.08)	67.94 (0.10)	71.96 (0.10)	1090, 1092
Daudmannsodden ²	78.12°N	1970	80.61 (0.46)	85.01 (0.45)	67.75 (0.57)	71.64 (0.67)	41, 37
Prins Karls Forland ²	78.20°N	1963	80.01 (0.46)	82.51 (0.53)	66.28 (1.22)	71.34 (1.00)	12, 14
Sassendalen ³	78.18°N	1963	83.41 (0.55)	88.44 (0.49)	67.81 (0.82)	72.87 (0.51)	21, 15
Gåsøyane, Gipsdalen ³	78.27°N	1980	83.69 (0.79)	87.34 (0.45)	66.65 (0.68)	71.92 (0.58)	20, 19
Kongsfjorden, Ny-Ålesund ³	78.55°N	1980	82.13 (0.17)	86.98 (0.17)	67.62 (0.17)	71.85 (0.18)	304, 334

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

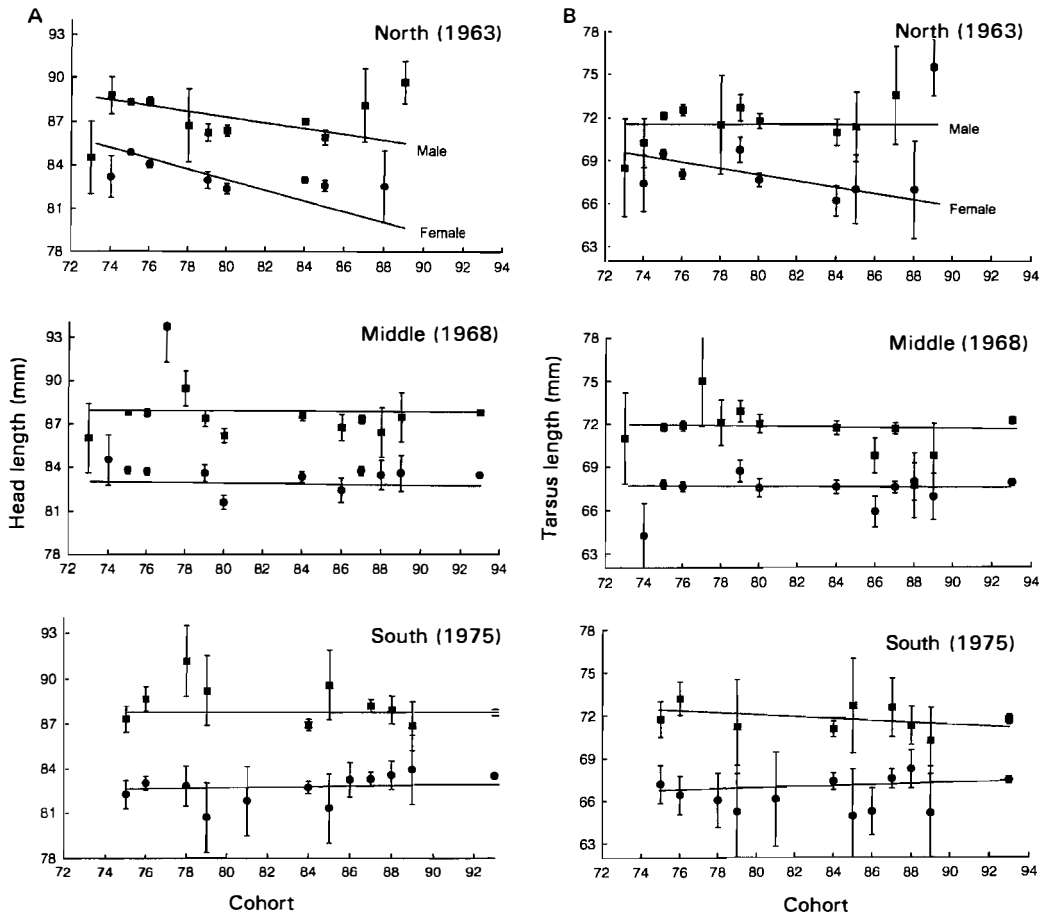


Fig. 4. Variation in A head and B tarsus length for three sub-colonies on Nordenskiöldkysten; males (squares), females (dots). Northern colony (a): Overall difference between the sexes was significant (MANCOVA $F_{2,650} = 4.48$, $P = 0.012$) so the data were not pooled. There was a significant linear change with cohort for head length (females: ANCOVA $F_{1,505} = 41.99$, $P < 0.0001$; males: ANCOVA $F_{1,490} = 9.98$, $P = 0.002$) and for tarsus in females (females: ANCOVA $F_{1,79} = 11.70$, $P < 0.001$; but not in males: ANCOVA $F_{1,79} = 0.0009$, $P = 0.974$). Middle colony (b): Pooling over sexes, no significant linear change in size was detected across cohorts (overall size, MANCOVA $F_{2,1110} = 1.32$, $P = 0.268$; head length, ANCOVA $F_{2,1111} = 0.59$, $P = 0.441$; tarsus ANCOVA $F_{2,1111} = 0.74$, $P = 0.389$). Southern colony (c): Pooling over sexes, no significant linear change in size was detected across cohorts (MANCOVA $F_{2,411} = 1.11$, $P = 0.329$; head length, ANCOVA $F_{2,412} = 1.75$, $P = 0.187$; tarsus ANCOVA $F_{2,412} = 0.05$, $P > 0.5$).

Discussion

With the increase in the Svalbard barnacle goose population, from 3,200 in 1970 to 23,000 in 1996 (Black 1998a), far more geese have been harvesting the sparse arctic vegetation. Prop *et al.* (1984) gives evidence from Nordenskiöldkysten that food depletion during the breeding season has a limiting effect on reproduction. When the first geese

through an area take most of the available food, the competition for the remaining food is intensified as the season progresses. Geese arriving at a patch that has already been visited by other geese have fewer items to choose from. In addition, the intake rate on previously grazed plants is much reduced (Prop & Loonen 1988). Plant depletion is greater when goose density increases.

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

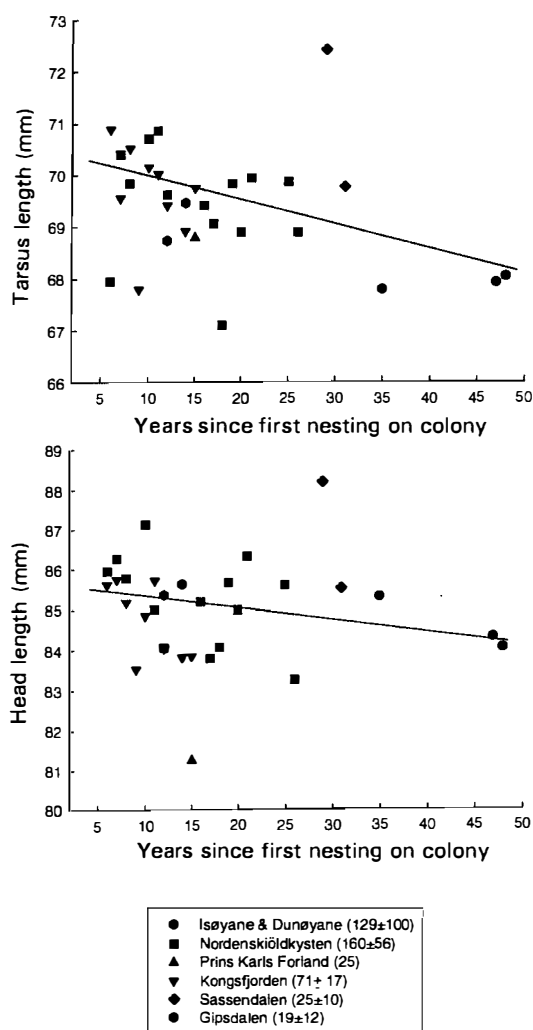


Fig. 5. Body size variation for six colonies of various ages. There was a highly significant decline in body size with colony age (overall MANCOVA $F_{2,3298} = 41.95$, $P < 0.001$); head length declined by about 0.03 mm/yr ($F_{1,3671} = 29.96$, $P < 0.001$), while tarsus declined by about 0.05 mm/yr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

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

the amount of food available per goose. Whereas body size has decreased substantially at Kongsfjorden, at Nordenskiöldkysten the decline is less steep and reflects numbers within sub-populations.

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

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

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

We favour the habitat saturation hypothesis rather than the alternative—an increasing mortality selection against large adults—because Cooke et al. (1995), after an extensive analysis, reported that adult body size did not influence survival. The

type and phenology of the plants are variables that may effect body size differences between colonies and which are related to the timing of the spring thaw (Prop & de Vries 1993). If geographic variation in vegetation phenology influences body size variation, we might expect larger-sized geese in warmer areas and vice versa.

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

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

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

declining structural size may well be ubiquitous among goose populations whose numbers have risen to unprecedented levels. This applies to the Swedish population of barnacle geese (Larsson & Forslund 1991, 1992; Larsson 1993), to lesser snow geese (Cooch *et al.* 1991 b), and to greater snow geese *Anser caerulescens atlantica* (Gauthier & Reed pers. comm.).

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

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

It remains to be seen whether geese of the genus *Branta* will degrade arctic vegetation to the same degree as has been done by snow geese. Habitat degradation in areas used by snow geese has been caused by the geese feeding on underground plant

parts, which kills the plant (Cooke et al. 1995). This behaviour is less common in *Branta*. Perhaps goose-plant interactions are more stable with *Branta*; two of four populations that we report had stable body sizes over periods exceeding a decade. *Branta* species typically graze on above-ground plant parts, a factor that might be expected to bring the population more gradually into balance with habitat carrying capacity. This contrast in *Branta* and *Anser* foraging behaviour might influence our interpretation of population dynamics in the two goose types.

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Breeding success of cliff-nesting and island-nesting barnacle geese in Svalbard

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Compared to island-nesting barnacle geese *Branta leucopsis*, adult females nesting on nearby cliffs showed 13% lower average reproductive success. Ringed barnacle goslings from cliff-nesting sites showed 8.6–16.9% lower survival rates (significant in one year out of two). Despite these disadvantages, cliff-nesting appears to be a useful alternative to island-nesting, which may be limited in Svalbard and at a premium. Surprisingly little is known about the number of cliff-nesting geese in Svalbard and their impact on population dynamics. The abundance of cliffs and canyons in Svalbard and the potential for barnacle geese to exploit this breeding habitat merits further study.

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Introduction

Nesting on cliffs is common for barnacle geese *Branta leucopsis* in Greenland and Russia, but relatively rare in Svalbard (Owen 1980; Cabot et al. 1984; Prestrud et al. 1989). Reports from early explorations in Svalbard indicate that cliff-nesting barnacle geese were once common. The most famous cliff-nesting colony was outside the town, Longyearbyen, where birds were recorded between 1907 and 1921 (Norderhaug 1984). In those days, the western islands of Spitsbergen that currently support barnacle goose colonies were occupied by the light-bellied brent goose *Branta bernicla hrota* (Norderhaug 1970).

The once endangered Svalbard barnacle goose population has increased in number from a low of 300 birds in 1948 to 23,000 in 1997 (Black 1998a). The reasons for the initial increase were related to reduced exploitation throughout the range and the birds' use of improved agricultural pastures at Caerlaverock (Owen & Norderhaug 1977). The increase in numbers in the 1980s resulted in an expansion in range, notably on the breeding grounds where the number of colonies have tripled (Prestrud et al. 1989; Mehlum 1998, this volume)

and, in the 1990s the size of some well-established colonies apparently doubled in size (Drent et al. 1998, this volume).

A favoured hypothesis for the continued increase in population size is due to the success of birds that colonise new nesting areas, like those in Kongsfjorden (Black 1998b, this volume). Whereas the discovery of additional offshore islands seems limited, expansion to the multitude of cliffs and canyons of Svalbard may improve breeding opportunities for individuals that are not established on the offshore islands.

Cliff-nesting is renowned for its hazards, including the initial jump from nest ledges by young goslings, and heavy predation, mainly from arctic foxes *Alopex lagopus* and glaucous gulls *Larus hyperboreus* (Cabot et al. 1984). If cliff-nesting geese in Svalbard are able to recruit offspring despite the obstacles, then perhaps this nesting strategy has contributed to the continued growth of the population.

In this paper we compare the relative breeding success of the two nesting strategies. We focus on two adjacent colonies located in eastern Isfjorden. We have been particularly interested in addressing three questions: (1) How does the nesting phenology differ between the two nesting strate-

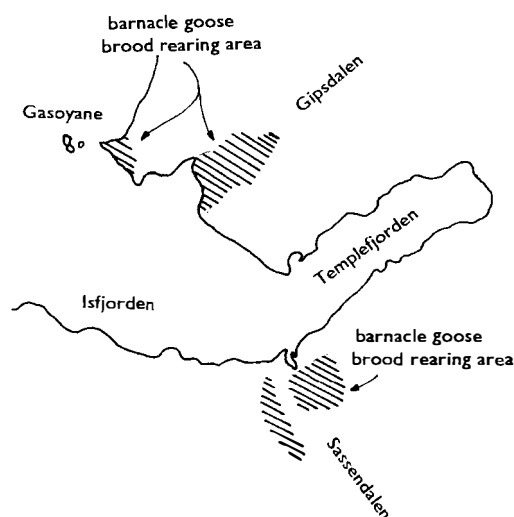


Fig. 1. Location map of eastern Isfjord showing Sassendalen, Gipsdalen, principal breeding and brood-rearing areas of barnacle geese.

gies? (2) Is cliff-nesting a profitable reproductive strategy in the 1990s in Svalbard? (3) Is it possible that cliff-nesting geese help fuel the growth of this population?

Study area and methods

Sassendalen ($78^{\circ}18'N$ $17^{\circ}00'E$) and Gipsdalen ($78^{\circ}25'N$ $16^{\circ}30'E$) are low-lying glaciated valleys running into Sassenfjorden at the eastern end of Isfjorden (Fig. 1). Much of the valley bottoms lie between 10 m and 40 m a.s.l. and are characterised by glacial erosion and deposition forming extensive networks of fluvial sediments, river fans, shallow streams and bogs. In Sassendalen, barnacle geese breed on cliff ledges within the valley itself and on tributary valleys (e.g. Nøisdalen, $78^{\circ}23'N$ $17^{\circ}15'E$). Nests have been found at 300 m a.s.l., although most are between 100 m and 250 m a.s.l. The first documented nesting attempt in Sassendalen was in 1963 (Prestrud *et al.* 1989) and colony surveys have indicated ca. 40 nests there in the 1970s, increasing to 75 in 1984 and up to 100 nests in 1988 (Prestrud *et al.* 1989). The barnacle geese that summer in Gipsdalen bred on Gåsøyane ($78^{\circ}27'N$ $16^{\circ}12'E$), a 50-ha island. The colony is

relatively new with the first breeding recorded in 1982 (Prestrud *et al.* 1989). Numbers have increased here, with an estimated 3–8 nests in the early 1980s, 30 in 1985 (Prestrud *et al.* 1989) and c. 130 nests in 1993 (H. Solheim pers. comm.) Extensive surveys of Gipsdalen in 1989 did not record any nesting attempts in the valley itself (Syvertsen 1990). The brood-rearing areas in Gipsdalen and Sassendalen are approximately 20 km apart. We think it highly unlikely that barnacle geese nesting in Sassendalen moult in Gipsdalen and vice versa.

Studies of cliff-nesting barnacle geese were carried out from mid-May to the end of June in both 1992 and 1996. Flocks of moulting non-breeders and families were rounded up in each of the two valleys in late July and early August in both 1993 and 1995. The age of each goose was determined as adult, gosling or yearling, based on plumage characteristics and sexed by eversion of the cloaca. A metal ring was put on one leg and an engraved plastic ring on the other. Each bird was weighed to the nearest 25 g using a 5 kg balance. The weight of each gosling was standardised to 1 August (after Owen 1986) to allow for differences in catch dates. In 1995, each gosling was assigned an age class on a scale of 1 through 6 according to plumage development (1 = less than 1 week old, 2 = 1–2 weeks, 3 = 2–3 weeks, 4 = 3–4 weeks, 5 = 4–5 weeks, 6 = 5–6 weeks old, after Owen 1986). This feature can be used to reliably determine hatch date, but note that age and weight are not entirely dependant.

Observations of colour-ringed individuals were obtained from the winter quarters on the Solway Estuary in northern Britain (ca. $55^{\circ}N$ $3^{\circ}W$) in 1993/94 to 1995/96, and during summer fieldwork in both valleys in Svalbard in 1994. On the Solway Estuary, the chances of resighting an individual were found to be around 95% annually (Owen 1982). Each time an individual was observed, the date, location and flock size was noted, and an attempt was made to determine any family relationships. Multiple observations during the winter season enabled a reproductive success score (the number of goslings per female) to be determined for all individually-marked adult geese (Black & Owen 1989; Owen & Black 1989). Survival of ringed goslings was also based on sightings; an individual ring needed to be read twice to be classed as alive, or once if the gosling was seen with known family members (see Black & Loonen unpubl. data). Reproductive success

was analysed using a Poisson error structure in GLIM (Crawley 1993) with year and colony treated as factors.

Results

Nesting phenology at cliff-nests

Barnacle geese arrived back at cliff ledges in Sassendalen on 21 May 1992 and 19 May 1996, and nest initiation occurred during the following two weeks. Assuming that incubation took ca. 25 days (Owen 1980), incubation commenced between 3 and 15 June. The earliest goslings were seen on 28 June, with most young hatching between 4 and 10 July ($n = 12$ nests).

Behaviour during exodus at cliff-nests

Once hatched, the goslings were highly mobile, exploring the ledge on several occasions before returning to the nest. The length of time between hatching and jumping ranged from 24 to 50 hours. The jump was usually initiated by the adult male, which, on most occasions, slid down the ledge and upon losing his footing, glided down to the tundra below, where he would be joined by the adult female and then the chicks. The ability to negotiate the exodus down the cliff face varied considerably among parents and goslings. Twelve 'jumps' were observed between 03:19 and 16:21 hrs. In seven cases, involving broods of two to four goslings, the parents initiated the exodus by flying to the bottom of the cliff and calling up at the goslings or giving pre-flight signals. The goslings jumped or slipped off the nest ledge and landed at the bottom after tumbling and bouncing off rocks on the way down. In another case, one of four goslings slipped off the ledge, and fell to the gorge floor. The parents immediately flew down to join the gosling and the remaining three jumped and tumbled down (all survived). In another case, three of four goslings were unable to arrest their momentum from the jump; they fell to the base of the cliff and into a river below where they were abandoned. The parents returned to the ledge to attend the lone gosling – the latter jumped the following day and

survived. From another brood of three, a parent male accidentally knocked one gosling off the cliff ledge, another was taken by a glaucous gull, and the third perished after jumping into a waterfall. In another case, parents of a brood of two deserted their goslings on the nest ledge as four glaucous gulls approached; one gosling was taken by the gulls and the other scrambled down the scree and was later seen with the parents. At another nest, four goslings initiated the exodus, climbing a vertical scree slope while the parents watched from the nest ledge (three of four survived).

Early gosling mortality at cliff-nests

Of 37 goslings from 12 nests observed, 6 (16.2%) were killed on the scree below the cliff or were washed away in the river and abandoned, 3 (8.1%) were taken by an arctic fox and 5 (13.5%) were taken by glaucous gulls. The 23 (62.1%) goslings that survived were seen to bounce and spin off rocks below the nesting ledges, yet they were capable of running to their calling parents on the valley bottom immediately after making the jump. Two of the 23 goslings were noticeably weakened by the impact of the fall and had to struggle thereafter to keep up with the family group.

Gosling age and weight at ringing

In the two ringing years, 580 barnacle geese were trapped, of which 163 goslings were newly-ringed. The mean age class of goslings ringed in Gipsdalen (approximately 2–3 weeks old) in 1995 was similar to those ringed in Sassendalen (Table 1). The mean weight of goslings ringed in Gipsdalen was similar to those ringed in Sassendalen in both 1993 and 1995 (Table 1).

Brood size

Observations during the brood rearing period showed that mean brood sizes were larger, although not significantly so, in Gipsdalen compared with Sassendalen in both 1993 and 1994 (Table 1).

Table 1. Barnacle gosling age classes, weight, brood sizes and reproductive success of breeding-age females in Sassendalen (cliff-nesting) and Gipsdalen (island-nesting), 1993–1995.

	Sassendalen			Gipsdalen			Anova	P
	Mean	s.d.	sample size	Mean	s.d.	sample size		
Gosling age class								
1995	3.09	0.40	44	3.36	0.86	35	3.53	ns
Gosling weight								
1993	916 g	283 g	33	834 g	171 g	85	3.65	ns
1995	979 g	124 g	43	932 g	192 g	36	1.71	ns
Brood size								
1993	2.08	0.82	7	2.71	1.44	20	2.17	ns
1994	2.11	1.05	9	2.77	1.26	56	0.17	ns
Average reproductive success of breeding-age females								
1993 and 1995 combined	0.39		96	0.52		493	$\chi^2=35.81$	ns

Average reproductive success

From observations made during the winter months in Scotland, and controlling for year of capture, reproductive success was significantly higher for island-nesting geese (Gipsdalen) compared with cliff-nesters (Table 1). In addition, the percentage of adult females that had successfully bred was higher, although not significantly so, for geese caught in Gipsdalen compared to those caught in Sassendalen (Table 2).

Gosling survival

Winter sightings of goslings in Britain revealed a

significantly higher survival rate for those ringed in Gipsdalen than those ringed in Sassendalen in 1993, but no significant difference was recorded in 1995 (Table 2).

Discussion

Geese endeavour to nest as early as possible so their young have sufficient time to fledge and procure reserves for migration in the short arctic summer (review in Owen 1980) since the chances that goslings will fledge decreases with the date of egg laying (Cooke *et al.* 1984; Sedinger & Raveling 1986). In our study, Gipsdalen goslings were similar in both age class and weight to those

Table 2. Percentage of breeding-age female barnacle geese recruiting young and barnacle gosling survival in Sassendalen (cliff-nesting) and Gipsdalen (island-nesting), 1993–1995.

	Sassendalen		Gipsdalen		G _{adj}	P
	%	n	%	n		
% of breeding age females recruiting young						
1993	8.0	25	19.0	168	2.07	ns
1995	28.6	42	31.8	117	0.17	ns
Gosling survival						
1993	66.7	12	75.3	93	7.69	<0.01
1995	46.6	28	63.3	30	1.64	ns

hatched in Sassendalen. It would appear that local climate effects, in particular, the late clearance of snow from higher cliff ledges and proximity of the cliff-nest sites to the relatively milder coastal areas did not delay clutch laying in either year studied. However, other cliff-nesting sites, especially those at higher altitudes or those some distance from the coast, may experience later snow cover than islands and this may affect the timing of egg laying.

Geese nesting on Gåsøyane were free from predation by arctic fox. The presence of large gulls and skuas is probably similar in both breeding areas. However, gosling deaths from jumping from cliff nests and associated predation are in addition to the losses suffered by island-nesters. Once at the base of the cliffs, goslings are led to brood-rearing areas, and predation pressure thereafter may be similar for either island or cliff-nesting broods. The losses due to the cliff jump (and associated predation) reported during this study (38% of goslings from 12 nests) are similar to those reported in Greenland, where 44% of goslings from 30 nests were killed due to the jump and immediate predation (Cabot et al. 1984).

In Greenland, most nesting attempts occur on cliff ledges. The key sites thaw early and are close to brood rearing areas. The availability of suitable cliffs does not appear to be limiting (in Greenland); however, some cliff colonies were far more productive in terms of successful nests (e.g. 83% at Kap Seaforth) than others (e.g. 28% at Didrik Pining, Cabot et al. 1984). Although there are many potential cliff-nesting areas in Svalbard, proximity to good brood rearing areas, predator density and access to water to escape from land predators may limit the suitability of many of these.

Despite the two primary disadvantages of nesting on cliffs (a potential delay in commencing egg laying and increased gosling mortality through jumping), the consequential impact is limited to 13% lower reproductive success of adult females (Table 1) and 8.6–16.9% lower survival rate of goslings (Table 2, significant in one year out of two.)

Relatively little is known about the number of cliff-nesting barnacle geese in Svalbard and their impact on population dynamics. Cliff-nesting appears to be a successful alternative to island-nesting providing the distance from suitable brood-rearing areas is not too great.

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Growth of the Svalbard barnacle goose *Branta leucopsis* winter population 1958–1996: An initial review of temporal demographic changes

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We examine the temporal pattern in fecundity and survival data obtained from annual counts of the Svalbard barnacle goose population over-wintering on the Solway, United Kingdom, for the period 1958/59–1996/97. The population has increased in size from around 1000 individuals in the late 1950s to in excess of 23,000 birds in 1996. The intrinsic population growth rate ($\ln(N_{t+1}/N_t)$) has averaged 0.077 over this period – approximately equivalent to 8% annual growth, although a robust regression through all the count data suggests a growth of closer to 5%. However, different phases in growth can be recognised (1958–1963; 1971–1980; 1993–1996) when the annual rate was greater than 10%, with the remainder where growth was less than 5%. All measures of fecundity exhibited a pattern of relatively high values in the 1950s and 1960s, a decline through the 1970s, followed by a period of apparent stability through the 1980s at some much lower value compared to the 1950s and 1960s, a trend that has largely continued into the 1990s. Current estimates over the past ten years (1987–1996) of the proportion of juveniles, mean brood size and productivity are 0.125 ± 0.014 , 1.866 ± 0.063 and 0.166 ± 0.022 respectively. Annual survival estimates, on the other hand, increased through the late 1950s, 1960s and early 1970s, with a suggestion of an increase across the course of the whole study period ($P = 0.06$), and a significant increase post-1979. Current estimates of survival are in excess of 0.90. Plots of annual fecundity values (percentage juveniles, brood-size, breeding ratio and productivity) against lagged population size (i.e. N_{t-1}) indicated statistically significant declines with increasing population size, consistent with a density-dependent reduction in fecundity. However, significant quadratic fits to some of these data are suggestive that these declines have stabilised at some new, lower level, and in some instances have increased post-1979. We ascribe this latter stabilisation and/or increase to the expansion of new breeding colonies away from the 'traditional', older sites, the latter probably continuing to show strong density-dependence in fecundity. Survival estimates were independent of lagged population size. We suggest that various conservation measures in the 1950s, 1960s and 1970s allowed the population to reach an equilibrium level in the latter decade, prior to parts of the population being released from density-dependence post-1980, when range expansion and the development of new breeding colonies has resulted in further population growth.

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Introduction

This paper reviews the increase in population size over the past 40 years in the population of the barnacle goose *Branta leucopsis* that breeds on Svalbard at 74–80°N and winters in temperate

habitats on the Solway Firth, northern Britain. The population has been counted annually upon arrival on the wintering grounds since 1957 by the Wildfowl and Wetlands Trust (WWT). The census data include the total numbers of geese that reach the wintering grounds on the Solway, the proportion of juveniles (first-year birds) present in the

flocks, and the mean brood-size (i.e. the number of young in each family unit). From these three variables it is possible to calculate various fecundity and survival figures on an annual basis. Two major analyses of these life-table data have been undertaken: Owen & Norderhaug (1977) examined the data for the period 1948–1976, and Owen (1984) extended these analyses to include the 1983 results, as well as examining the reproductive success and survival of individually ringed birds (see also Owen 1982). In their discussions of the trends in the population size, the initial increase in numbers in the early 1960s was attributed to the various conservation measures initiated in the 1950s when legal protection was given to birds both on their wintering and breeding grounds, and the first winter refuge created. However, between 1964 and 1970 the population was remarkably stable at around 3500, a fact thought to be determined by an annual mortality estimate of around 25%, much of which was considered to be due to continued illegal hunting on the wintering grounds (Owen 1982). The subsequent increase in the 1970s coincided with the creation of a further refuge area on the Solway by WWT in 1970, cessation of shooting in Norway and protection of breeding colonies on Svalbard, these last two being legislated for in 1971 and 1973 respectively. Owen (1984) has argued that it was the creation of an additional safe haven at Caerlaverock, on the Solway, that allowed the subsequent population increase, as the geese were now able to feed relatively unmolested during the open hunting season on wildfowl in winter. The fact that mortality fell to around 10% at this time supports this hypothesis, although Owen (1984) considered that some 300–400 birds continued to be illegally shot each winter in the early 1970s. In addition, the legal protection given to the main breeding colonies on Svalbard meant that these offshore islands could not be visited by humans, thereby minimising disturbance and the concomitant predation of clutches by gulls and skuas.

Owen & Norderhaug (1977) were unable to establish density-dependent factors affecting either fecundity or mortality schedules for the data up to 1976; however, the subsequent analyses by Owen (1984) indicated a reduction in the proportion of successful breeders (i.e. pairs returning with at least one young to the wintering grounds) as the number of potential breeders (pairs of breeding age) increased. Similarly, Owen

(1982) was unable to establish density-dependent mortality from resighting and recovery data of individually marked birds, but subsequent analyses (Owen & Black 1989, 1991), with longer runs of data, found that density-dependent effects were apparent, especially over the autumn migration period. In addition to an increase in adult mortality, they showed that in some years as much as 40% of the goslings were failing to return to the wintering grounds, these young being lost between one to four months of age. The smaller, less well-developed goslings suffered higher losses. Prop *et al.* (1984, Figs. 28–29), describing the foraging performance of different brood sizes and hence dominance classes, provided the first hint that competition for food during the brood rearing period may be affecting the ability of the individual young to gain adequate fat and nutrient reserves for the return journey. Current analyses (Pettifor & Black unpubl.) indicate continued declines in both reproductive success and survival of individually ringed birds with increasing population size.

This paper describes the changes in population size, and the annual survival and fecundity, of the Svalbard barnacle goose population over the past forty years. The population currently numbers over 20,000 birds. Owen & Norderhaug (1977) and Owen (1984) have described the population changes from the low numbers in the late 1940s through to the mid-1970s and early 1980s respectively. Here we review these earlier data, but concentrate on the data from 1980 onwards, in particular with a view to understanding the current dynamics of the population.

Methods

Estimates of total population size have been collated since the winter 1957/58. Pre-1970 census data are based on maximum counts which were conducted at least once per winter (Owen & Norderhaug 1977). Post-1970 counts were made on a daily basis from the towers at Eastpark Farm, Caerlaverock, with periodic ground counts over the whole of the wintering range on the Solway made in October and/or November (see Owen & Norderhaug 1977). In addition to flock counts, two additional parameters were recorded annually after the majority of the population had arrived in

autumn, namely mean brood-size and the percentage juveniles. These were recorded when the entire population was present at the Caerlaverock reserve in order to obtain a representative sample of the population as a whole. Errors in these data were thought to generally be less than 1% from 1971 onwards (Owen 1984). As the wintering distribution expanded with increasing numbers, the count effort was increased (Owen et al. 1987). Co-ordinated censuses were required to exclude the possibility of double counting between sites. Counters were placed throughout the 1250 km² range and counts were made at the same time at each site. These counts have been augmented since 1990 by fortnightly counts, made by following a prescribed route by car to all major haunts (after Shimmings et al. 1992). In recent years the maximum counts were achieved during spring censuses, indicating that numbers built up gradually during the winter. In 1996/97 we found that the proportion of juveniles also increased from 12.1% in October/November ($n = 12,000$ birds aged) to 15.1% in December (11,000 birds aged), suggesting that progressively more family groups have been arriving on the Solway later in the season as the study has continued. Therefore, since 1991 the co-ordinated census totals from the Solway have been revised to include counts from the network of field workers continuing to monitor throughout the winter those areas where barnacle geese have been recorded during the migratory period. We also adjusted the maximum counts and the proportion of juveniles achieved in 1991–1994 by assuming that a further three percent of juveniles arrived late (Black et al. in press).

These basic count data collected annually each winter (total population size: N_t , proportion juveniles: PJ_t , and mean brood-size: BS_t) allow the following life-table parameters to be calculated:

1. Lagged Population Size (N_{t-1}): in year t , this is the total population size in year $t - 1$.

2. Number of Juveniles (J_t): the total number of juveniles arriving in Britain each winter is calculated as:

$$J_t = PJ_t \times N_t$$

3. Breeding Success (R_t): the number of successfully breeding adults in the population can be calculated as:

$$R_t = 2 \times (J_t / BS_t)$$

4. Potential Breeders (A_t): the number of potential breeding birds in the population is estimated to be equivalent to the number of adults in the population, defined here as the number of birds in their third year or older. The number of birds in their second year, Y_t , can be calculated as:

$$Y_t = J_{t-1} - \times S_{t-1}$$

where S_t is the survival rate from year $t - 1$ to year t (see Point 7 below). The number of adults is thus calculated as:

$$A_t = N_t - J_t - Y_t$$

5. Breeding Ratio (PB_t): the proportion of potential breeders that were recorded as having successfully bred in year t upon their return to the wintering grounds. This is calculated as:

$$PB_t = R_t / A_t$$

6. Productivity (F_t): the proportion of juveniles to adults in the population in year t ; i.e.:

$$F_t = J_t / A_t$$

7. Survival Rates (S_t): the annual crude survival rates can be estimated as:

$$S_t = (N_t - J_t) / N_{t-1}$$

Note that survival rates estimated in this manner from census counts will be underestimated in some years and overestimated in others, but it is assumed that these errors are self-compensatory over time (e.g. Owen 1982).

Statistical analyses

In this paper we are primarily interested in describing the patterns in the data over time and over various population densities, in order to establish temporal trends in the data and whether or not survival and fecundity schedules show any evidence of density-dependence. Local regression models are useful (see below) in visualising such variation in temporal trends, although establishing clear start and end points for any phases identified is difficult. M. Bell (in Kirby & Bell 1996) developed a statistical technique which attempts to fit a variable number of straight line segments to the data while minimising the residual deviance of models. However, use of this technique failed to allow statistically significant differences to be established between sequential runs of segments.

For example, segment analysis of the population time series fitting from three to seven segments gave deviance scores of 96.38, 95.76, 95.76, 94.60 and 95.76 respectively. Thus, while six segments resulted in the minimum deviance, change in deviance tests (approximating a χ^2 distribution) indicate that this option does not provide a significantly better fit than any of the alternatives. Thus, in order to describe both temporal trends and investigate potential density-dependence we have used three statistical approaches: (1) graphical inspection of the raw data, with subsequent fitting of linear, squared and cubic terms of the explanatory variable to the response variable; (2) non-parametric splinal smoothing and local regression models; and (3) robust regressions.

All models were fitted using S-plus Release 4.5.1 (MathSoft 1998). We have used these differing techniques as there is frequently no one 'correct' method of statistical testing (although there can be clear 'wrong' ways of analysing data), and hence the purpose of these specific analyses was not to test for the statistical significance or otherwise of each explanatory variable independently of the others, but rather to examine the trends in the data and obtain biologically meaningful parameter estimates.

A strict sequential approach was adopted in the fitting of the polynomials, since the high colinearity between the linear and the higher order terms prevented testing for significance of each term independently through deletion. While polynomial curves may adequately fit the data, in many instances the 'shape' of the curves are forced to that specified by the order of the polynomial, resulting in inappropriate fits to the data. Additive models, on the other hand, fit curves such that only a restricted set of adjoining points are used to determine the shape at each point of the curve (thus

their name, local regression curves). The cubic spline is one such approach to smoothing data. It relies on minimising the penalised residual sum of squares, with the smoothing function chosen through cross-validation. The advantage of these local regression models is that the fit is not 'forced' in the manner of polynomials and thus allows for the detection of plateaus in data which would not generally be picked up using polynomial regressions. We have also used robust regression techniques to validate our conclusions based on the other two statistical approaches discussed above. Since we are analysing data which are collected annually, we are unable to fit year effects as a categorical variable to control for between year stochastic variation (i.e. good and bad years in breeding success for example). Standard least squares regression is sensitive to both departure from normality of error structure, and outliers and their leverage. Robust regression techniques tend to fit lines which ignore such data points using a minimisation algorithm relating to iterative examination of the residuals. Details of these approaches are summarised in the S-Plus 4 Guide to Statistics (1997) and in more detail by Chambers & Hastie (1992) and Venables & Ripley (1994), who also provide further references.

Results

Growth of the Svalbard barnacle goose population over time

Fig. 1A illustrates the growth of the winter population of the Svalbard barnacle goose since 1958.

Table 1. Parameter estimates and their standard errors derived from linear regressions for each of the phases of the Svalbard barnacle goose population as illustrated in Fig. 1B, plus that of the robust regression across all years (bottom row), and the intrinsic growth rates for each of these periods.

Years	Parameter estimate	Standard error	<i>t</i> -value	P	Intrinsic growth rate
1958–1963	0.2258	0.0297	7.6062	0.0016	0.218 ± 0.029
1964–1970	–0.0094	0.0160	0.5918	NS	–0.041 ± 0.020
1971–1980	–0.1010	0.0081	12.5300	0.0000	0.104 ± 0.012
1981–1992	0.0407	0.0043	9.5066	0.0000	0.031 ± 0.007
1993–1996	0.1462	0.0109	13.4042	0.0009	0.139 ± 0.015
All years	0.0532	0.0019	27.6208	0.0000	0.077 ± 0.001

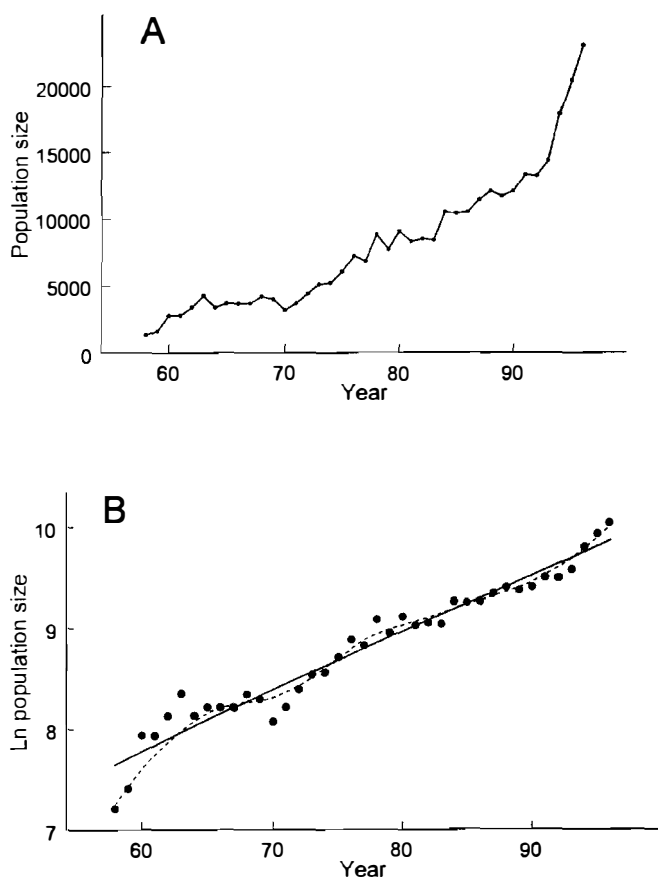


Fig. 1. A. Growth of the Svalbard barnacle goose population over time. B. The natural log of population size is used, with two different models fitted: the solid continuous line is a splinal fit, while that from a robust fit is shown as a broken line. As discussed in the text, the growth of the population has been divided into five phases, corresponding to the turning points of the splinal fit. These phases are indicated by the vertical broken lines. The linear regressions through each of these segments are also shown.

From a low of 300 in 1948 (see Owen & Norderhaug 1977), the population had grown to over 1000 birds by the late 1950s, and by 1980 it had reached 10,000 individuals. By 1990 the population was still below 15,000 birds, but a rapid increase in population size then occurred between 1993 (when the winter count stood at 14,350) and 1996 (when the population had reached 23,000 birds). The most recent series of counts (winter 1997/98) give a maximum of 23,800 individuals. Fig. 1B shows a series of fits to the natural log of population size plotted against time: the robust linear regression shows a mean annual growth of 5% between 1958 and 1996, while the splinal fit, which tracks the observed data much better, indicates five phases in the growth of the population over this period, namely three sections of strong growth (1958–1963; 1971–1980; and 1993–1996) and two sections of lower growth (1964–1970) and (1981–1992). Linear regressions have been fitted to these

sections in Fig. 1B, and their respective slopes are given in Table 1. Successive slopes differ significantly from each other (i.e. slopes 1 ν 2, 2 ν 3 . . . 4 ν 5) with t -values of 4.328, 5.129, 4.468, 2.920 (all $P < 0.05$) respectively.

Temporal pattern in the annual intrinsic rate of population growth

The temporal pattern in annual population growth rate, defined as $\ln(N_{t+1}/N_t)$, shows no significant linear trend between 1958 and 1996 (Table 2), although a splinal fit to the data and a robust regression indicate a significant positive slope post-1979. The mean annual growth for the 39 years (1958–1996) was 0.0768 ± 0.0223 , while pre-1980 this value was 0.0864 ± 0.0363 and post-1979 was 0.0644 ± 0.0212 . A two-sample unequal

Table 2. The results of linear and robust fits of the differing response variables on year (either all years, or 1980–1996 only).

Response	Linear fit					Robust fit				
	Estimate	s.e.	t	P	r ²	Estimate	s.e.	t	P	r ²
All years										
% juvs.	−0.0045	0.0015	3.068	0.0040	10.4	−0.0026	0.0015	1.768	0.0850	9.7
Brood-size	−0.0177	0.0045	3.964	0.0003	31.4	−0.0175	0.0069	2.527	0.0159	32.8
Breeding ratio	−0.0060	0.0022	2.718	0.0100	15.0	−0.0052	0.0053	0.991	0.3280	12.3
Productivity	−0.0094	0.0031	2.997	0.0049	21.2	−0.0048	0.0026	1.814	0.0780	14.5
Survival	0.0034	0.0018	0.915	0.0632	12.6	0.0017	0.0009	1.838	0.0741	5.4
Growth rate	−0.0015	0.0020	0.778	0.4412	14.0	−0.0014	0.0017	0.834	0.4095	12.4
1980–1996										
% juvs.	−0.0009	0.0031	0.298	0.7698	6.3	0.0036	0.0068	0.537	0.5994	4.8
Brood-size	−0.0410	0.0096	4.261	0.0007	19.5	−0.0410	0.0117	3.504	0.0032	21.9
Breeding ratio	0.0025	0.0040	0.610	0.5508	5.3	0.0045	0.0066	0.691	0.4999	4.1
Productivity	−0.0014	0.0047	0.289	0.7764	9.7	0.0056	0.1032	0.054	0.9573	6.7
Survival	0.0064	0.0025	2.562	0.0217	5.0	0.0036	0.0016	2.261	0.0390	2.5
Growth rate	0.0053	0.0043	1.248	0.2312	8.6	0.0119	0.0033	3.647	0.0024	6.2

variance *t*-test between the annual growth rates for these two periods does not reveal any significant difference ($t = 0.525$, NS). The differing growth rates of the five phases in population growth illustrated in Fig. 1B are given in Table 1.

Temporal patterns in annual fecundity and survival rates

All fecundity values have shown a decline over time (Fig. 2), while survival post-1970 has remained relatively constant. Each is discussed in detail below.

Proportion juveniles

There has been a significant linear decline (Table 2) in the annual estimates of the proportion of juveniles in the population obtained on their wintering grounds on the Solway (Fig. 2). Quadratic and cubic fits did not improve the model ($\Delta F = 3.647$ and 0.402 respectively). From a mean value (\pm s.e.) of 0.24 ± 0.04 between 1958 and 1969 inclusive, the proportion of juveniles dropped to 0.21 ± 0.04 for the years 1970–1980 and declined further to 0.13 ± 0.01 over the remainder of the study (1981–1996). Note that if the three ‘failed’ breeding years are excluded

(1977, 1979, 1981), the respective mean values for these three periods are: 0.24, 0.25 and 0.13. Inspection of the lines fitted to the data (Fig. 2) indicate a steady decline; however, inspection of Fig. 3 and the statistical analyses in Table 2 indicate that the slopes post-1979 do not differ significantly from zero. In fact, the splinal fit to these post-1979 data suggests a slight upturn more recently in the proportion of juveniles (corroborated by the most recent 1997/98 estimate of 16.8% juveniles for this last year).

Mean brood-size

There has been a significant linear decline (Table 2) in annual mean brood-size over the course of the study, which was also evident for the period 1980–1996. Thus between 1958 and 1969 inclusive the mean value (\pm s.e.) with respect to brood-size was 2.38 ± 0.11 , dropping to 2.27 ± 0.12 for the years 1970–1980 and declining further to 1.99 ± 0.06 over the remainder of the study (1981–1996) (Figs 2 and 3). There was no evidence of curvilinearity from polynomial fits to these data (quadratic and cubic fits: $\Delta F = 0.067$ and 2.834 respectively). The decline post-1979 was statistically significant (Table 2), although the splinal fit in Fig. 3 is suggestive that the decline may be slowly flattening out in more recent years. However, any such plateauing effect is very gentle, such that the latest

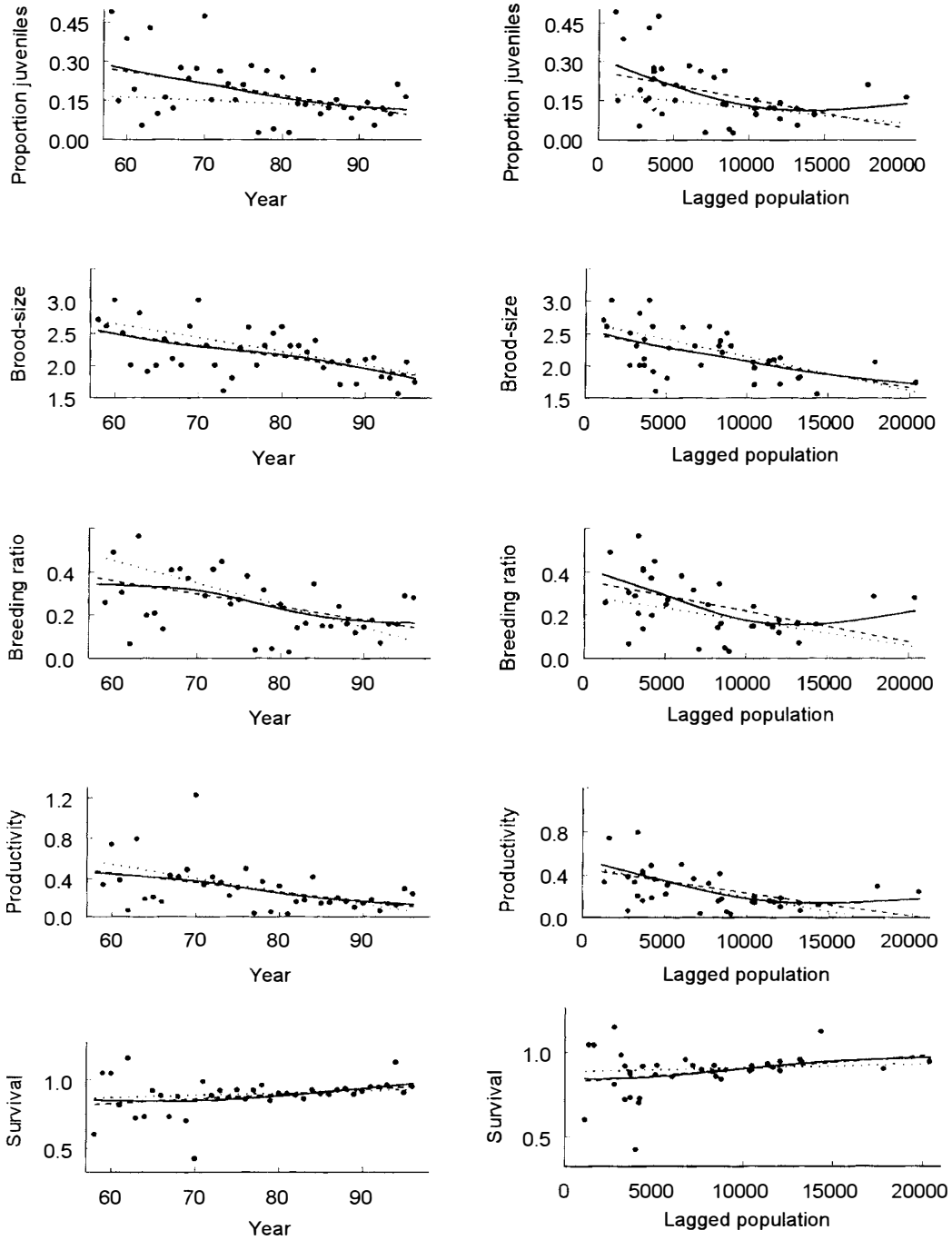


Fig. 2. Plots of the fecundity measures and survival against time and lagged population size (i.e. N_{t-1}). The curves represent three different fits: local regression model (solid line); linear model (heavy broken line); and robust regression model (lighter broken line).

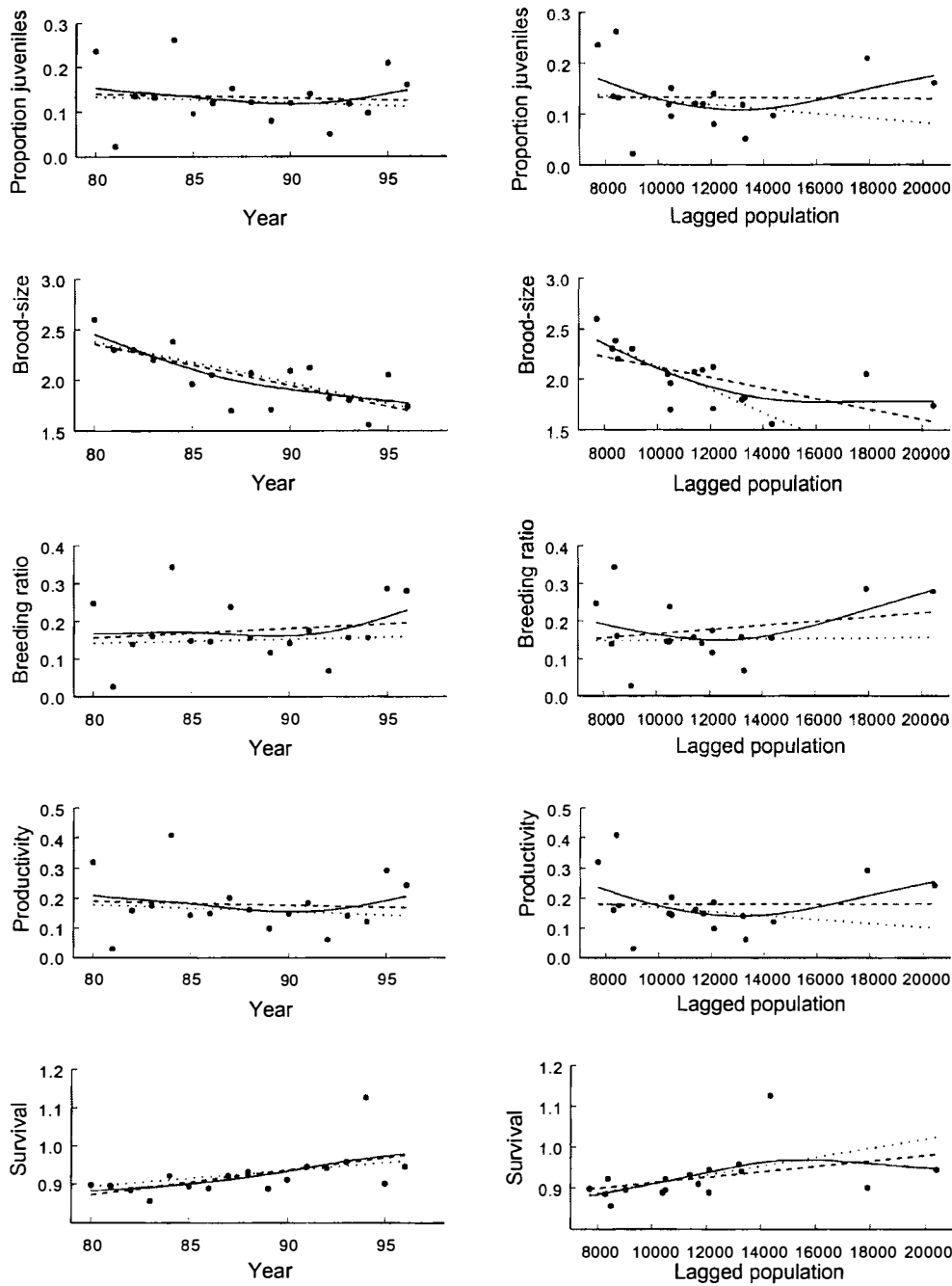


Fig. 3. As for Fig. 2, except the data were restricted to post-1979.

estimate of mean brood-size (i.e. for the 1997/98 season) of 1.76 could be consistent with either the linear or curvilinear models (see Fig. 3).

Breeding ratio

The ratio of actual to potential breeding adults has declined significantly over the course of the study when assessed using a least squares linear regression (Table 2, Fig. 2), but not when a robust model was fitted (Table 2), nor is there statistical evidence of an improved fit through the addition of quadratic or cubic terms ($\Delta F = 0.898$ and 0.227 respectively). However, Fig. 2 reveals a fall in the breeding ratio over the course of the study, from 0.28 ± 0.06 over the early years (1958–1969) to 0.15 ± 0.02 between 1981 and 1996. The splinal fit is also suggestive of this ratio plateauing from the mid-1980s (Fig. 3), supported by the lack of significant differences from zero in the slopes in the period post-1979 (Table 2).

Productivity

The number of juveniles per adult recorded upon their return in winter has declined significantly over time (Table 2, Figs 2 and 3): between 1958 and 1969 the mean value (\pm s.e.) was 0.36 ± 0.08 , declining to 0.29 ± 0.07 for the eleven years 1970–1980, and declining further since then (i.e. 1981–1996) to 0.15 ± 0.02 , with no evidence of curvilinearity in this response ($\Delta F = 1.067$ and 0.003 for the addition of quadratic and cubic terms respectively). However, post-1979, the fits to the data are not significantly different from zero, indicative that the decline has halted over this period, while the splinal plot suggests an upturn in productivity from 1990 onwards (Fig. 3).

Crude survival estimates

Survival rates over the first ten years of the study (1958–1967) averaged 0.860 ± 0.056 (mean \pm s.e.), while over the last twelve years (1985–1996) the mean was 0.94 ± 0.02 . The mean survival rate post-1990 is even higher, at 0.974 ± 0.04 ; however, this value is skewed owing to the

unrealistically high value of 1.126 obtained with respect to survival in 1994. Although crude survival estimates have increased over the course of the study (falling just outside the significance level of $P \leq 0.05$ for all years), they have increased significantly post-1979 as determined by both linear and robust fits (Table 2). Excluding the survival rate calculated for 1994, the mean value from 1980 onwards averages 0.912 ± 0.007 .

Patterns in annual fecundity, survival and intrinsic growth rates in relation to population size

If density-dependence were operative in this population, negative correlations would be expected between the various measures of fecundity and survival when plotted against density, the latter defined in this case as the lagged population size (i.e. N_{t+1}). All measures of fecundity have declined significantly with increasing lagged population size over the course of the whole study (Table 3, Fig. 2). However, the fits to the proportion of juveniles and the breeding ratio are significantly improved by the addition of the square of lagged population size, indicating a flattening out or even an upturn in these measures at higher densities (Table 4). The quadratic term for productivity is only marginally non-significant (Table 4). Post-1979, with the exception of brood-size, all other measures of fecundity do not show a slope significantly different from zero (Table 3), although all measures of fecundity (including brood-size) show a significant upturn at higher densities (Table 4, right-hand column in Fig. 3). From 1985 onwards, the slopes of the proportion of juveniles and mean brood-size do not differ significantly from zero, while the breeding ratio has a significant positive slope ($P < 0.05$), as does productivity at $P < 0.1$ (Table 3). Superficially these results are therefore not entirely consistent with a density-dependent decline in fecundity in that an upturn at higher densities would not be predicted. However, in all instances this result is due to two points recorded for the two highest densities. With the exception of mean brood-size, the robust fits indicate that none of the fecundity measures have slopes significantly different from zero, these results again being contrary to those

Table 3. The results of linear and robust fits of the differing response variables on lagged population size.

Response	Linear fit				Robust fit					
	Estimate	s.e.	t	P	r ²	Estimate	s.e.	t	P	r ²
All years										
% juvs.	—	3.668×10^{-6}	2.912	0.006	10.0	—	3.473×10^{-6}	1.735	0.091	9.8
Brood-size	—	1.110×10^{-5}	3.779	0.000	31.0	—	1.266×10^{-5}	3.362	0.001	36.0
Breeding	—	5.379×10^{-6}	2.661	0.001	15.0	—	6.742×10^{-6}	1.613	0.115	12.0
Productivity	—	7.656×10^{-6}	2.897	0.006	21.0	—	1.408×10^{-5}	0.884	0.404	13.0
Survival	6.933×10^{-6}	4.420×10^{-6}	1.795	0.081	8.0	2.819×10^{-6}	1.619×10^{-6}	1.741	0.089	2.3
Growth rate	—	4.888×10^{-6}	0.758	0.453	14.0	—	4.086×10^{-6}	0.624	0.536	13.0
1980–1996										
% juvs.	—	4.958×10^{-6}	0.067	0.947	0.0	5.874×10^{-6}	5.227×10^{-6}	1.124	0.278	10.0
Brood-size	—	0.165×10^{-5}	3.113	0.007	39.0	—	0.167×10^{-4}	3.075	0.008	35.0
Breeding	5.566×10^{-6}	5.880×10^{-6}	0.946	0.358	5.6	1.236×10^{-5}	1.009×10^{-4}	1.224	0.239	15.0
Productivity	1.745×10^{-7}	7.095×10^{-6}	0.024	0.980	9.7	—	2.162×10^{-4}	0.095	0.925	6.3
Survival	6.787×10^{-6}	0.406×10^{-5}	1.672	0.115	5.5	3.955×10^{-6}	3.397×10^{-6}	1.164	0.262	3.3
Growth rate	6.461×10^{-6}	6.408×10^{-6}	1.084	0.329	8.8	1.351×10^{-5}	1.511×10^{-5}	0.894	0.385	7.2
1985–1996										
% juvs.	0.649×10^{-6}	3.631×10^{-6}	1.787	0.104	3.7	6.497×10^{-6}	4.162×10^{-6}	1.561	0.149	3.8
Brood-size	—	1.878×10^{-5}	0.765	0.461	19.0	1.438×10^{-5}	2.086×10^{-4}	0.689	0.506	23.0
Breeding	1.298×10^{-5}	5.109×10^{-6}	2.540	0.029	5.3	1.583×10^{-5}	8.242×10^{-6}	1.921	0.083	4.1
Productivity	1.117×10^{-5}	5.247×10^{-6}	2.128	0.059	5.4	—	9.415×10^{-6}	1.779	0.105	5.3
Survival	4.676×10^{-6}	6.352×10^{-6}	0.735	0.479	6.5	2.386×10^{-6}	2.518×10^{-6}	0.947	0.365	3.6
Growth rate	0.125×10^{-4}	6.25×10^{-6}	1.998	0.073	2.9	1.078×10^{-5}	1.346×10^{-5}	0.801	0.441	2.4

Table 4. Significance tests of the inclusion of both linear and quadratic terms for lagged population size as explanatory variables of various fecundity measures, survival and intrinsic growth rate.

Response variable	Linear term		Quadratic term	
	t-value	P	t-value	P
1958–1996				
% juvs.	−3.1136	0.004	2.3283	0.026
Brood-size	−1.7085	0.096	0.6558	0.516
Breeding ratio	−3.0669	0.004	2.3739	0.023
Productivity	−2.7698	0.009	2.0098	0.052
Survival	0.4192	0.626	0.0168	0.987
Growth rate	−2.2015	0.034	2.0614	0.046
1980–1996				
% juvs.	−2.2748	0.039	2.2890	0.038
Brood-size	−3.6257	0.003	3.0804	0.008
Breeding ratio	−2.0637	0.058	2.2474	0.041
Productivity	−2.4550	0.027	2.4869	0.026
Survival	1.7522	0.102	−1.5099	0.153
Growth rate	−0.6240	0.543	0.7808	0.448
1985–1996				
% juvs.	−0.9685	0.358	1.1417	0.283
Brood-size	−0.5439	0.599	0.4777	0.644
Breeding ratio	−1.6493	0.133	1.9231	0.087
Productivity	−1.4059	0.193	1.6259	0.138
Survival	1.8264	0.101	−1.7590	0.112
Growth rate	−1.0734	0.311	−0.8938	0.394

expected if density-dependence were operating on productivity. However, taken over the whole time-frame (1958–1996), then the declines observed across all measures are consistent with a decrease in fecundity as population size has increased; the post-1979 results (where the data appear to be plateauing) could be interpreted as the population reaching its carrying capacity. This picture though is complicated by range expansion and the development of new breeding colonies (see the Discussion for an expansion of our thinking on the above brief summary of the results). With respect to survival, there is no significant trend with increasing densities in either direction (Tables 3 and 4).

Over none of the three time periods examined (all years, 1958–1996; 1980–1996 and 1985–1996) was it possible to establish a significant pattern for intrinsic growth rate when regressed against lagged population size (Tables 3 and 4). Plotting (N_{t+1}/N_t) against N_t is a traditional way of establishing density-dependence in populations: clearly, the above results do not provide any evidence of density-dependence. A more conser-

vative statistical test developed by Pollard et al. (1987) confirms this lack of density-dependence in this population for the years 1958–1996: $rdx = -0.259$, $P = 0.124$. However, see the above paragraph and the Discussion for further consideration of the difficulties in detecting density-dependence from ‘whole population counts’ when the population is made up of sub-populations which possibly are under differing constraints at different times.

Despite this lack of density-dependent limitation in the intrinsic growth rate of the population, growth rate itself tended to be positively correlated with annual fecundity and survival rates (an exception being a lack of any correlation with mean brood-size) – Table 5.

Correlations between the life-history table parameters

Over the length of the whole study period, the observed annual mean brood-size was positively

Table 5. The results of linear and robust fits of intrinsic annual growth rate on various explanatory variables 1958–1996, and below, 1980–1996.

Explanatory variable	Linear fit					Robust fit				
	Estimate	s.e.	t	P	r ²	Estimate	s.e.	t	P	r ²
1958–1998										
% juvs.	0.4403	0.1855	2.373	0.0229	13.2	0.9573	0.1671	5.730	0.0000	30.1
Brood-size	0.0584	0.0611	0.956	0.3454	2.4	0.0304	0.0821	0.369	0.7138	0.4
Breeding ratio	0.2053	0.1403	1.464	0.1520	5.6	0.6030	0.1289	4.679	0.0000	26.8
Productivity	0.1180	0.0979	1.204	0.2363	3.9	0.7599	0.0626	12.13	0.0000	37.0
Survival	0.5725	0.1484	3.858	0.0004	28.7	0.6921	0.1267	5.461	0.0000	20.7
1980–1998										
% juvs.	1.0697	0.2489	1.298	0.0006	55.2	1.1963	0.1336	8.953	0.0000	66.8
Brood-size	−0.0010	0.0808	0.011	0.991	0.0	−0.0010	0.0853	0.011	0.991	0.0
Breeding ratio	0.8566	0.1757	4.876	0.000	61.3	—	—	—	—	—
Productivity	0.6892	0.1625	4.241	0.000	54.5	0.7765	0.1137	6.828	0.000	64.0
Survival	0.8635	0.3159	2.734	0.015	33.3	0.9354	0.6128	1.526	0.1477	29.2

correlated with the annual proportion of juveniles recorded ($F_{1,37} = 24.87$, $P < 0.0001$), and independently with the breeding ratio ($F_{1,37} = 12.76$, $P < 0.001$). This suggests that in 'good' years more of the potential breeders were able to rear offspring, and of those which did breed, more were successful. This is evidenced by the positive correlation between the percentage of juveniles recorded and the breeding ratio in each year ($F_{2,36} = 471.9$, $P < 0.0001$), although note that here the quadratic fit is also significant (Table 6). Productivity was highly correlated with mean brood-size, the proportion of juveniles and the breeding ratio recorded annually. In each case a quadratic fit significantly improves the explanatory power of the model (Table 6). Post-1979, some of these above relationships are no longer statistically significant (Table 6).

Note that the only statistically *independent* comparisons possible are those between the proportion of juveniles and the mean brood-size since the other fecundity measures and the survival estimate are derived from these measures and total population size. Notwithstanding this difficulty, it is informative to examine the demographic changes over time (Fig. 4). The most noticeable feature is that both the absolute number and the proportion of non-breeders has increased over time ($F_{1,37} = 263.8$, $P < 0.0001$ and $F_{1,37} = 7.62$, $P = 0.009$ respectively), while, although the actual number of successful breeders has increased ($F_{1,37} = 27.15$, $P < 0.0001$), the proportion of these successful birds has significantly declined ($F_{1,37} = 5.116$, $P = 0.029$). Brood-size plotted against the number of successful breeders shows a negative trend (though not significant, $F_{1,37} =$

Table 6. Correlates between fecundity measures in the Svalbard barnacle goose, 1958–1996 and 1981–1996.

Response Variable	Explanatory Variable	1958–1996				1981–1996			
		Linear		Quadratic		Linear		Quadratic	
		t	P	t	P	t	P	t	P
Productivity	Brood-size	3.326	0.002	3.918	0.00004	1.178	NS	0.507	NS
Productivity	% Juveniles	19.41	0.0001	39.285	0.0001	106.1	0.0001	54.52	0.0001
Productivity	Breeding ratio	6.254	0.0001	3.578	0.001	13.257	0.0001	1.758	NS
% Juveniles	Breeding ratio	11.998	0.0001	2.382	0.02	15.165	0.0001	0.348	NS
Brood-size	% Juveniles	4.987	0.0001	1.723	NS	1.025	NS	1.553	NS
Brood-size	Breeding ratio	3.573	0.001	1.279	NS	0.207	NS	1.626	NS

3.429), and there is no pattern against the proportion of juveniles against successful breeders ($F_{1,37} = 0.624$). However, because the actual number of successful breeders has increased (if only marginally relative to the increase in total population size – see above), the number of juveniles reaching the wintering grounds each year has increased with a slope not significantly different from one ($F_{1,37} = 506.4$, $P < 0.0001$). Even ignoring the two most recent years (1995/96 and 1996/97) when 4,264 and 3,703 young respectively reached the wintering grounds, an average of 1483 juveniles were estimated for the five years 1990–1994 as compared to, for example, 1010 young produced for the period 1970–1974, and only 786 young at the start of the study (1960–1964). The one to one relationship illustrated in the bottom graph of Fig. 4 is partly a mathematical artefact brought about by the way both the number of young and the number of successful breeders is calculated (see Methods) – however, despite the declines in fecundity measures over time documented above, the increase in number of successful adults over time has resulted in increasing numbers of young appearing on the Solway each year (e.g. there is a highly significant relationship between the number of young regressed against year: $F_{1,37} = 16.69$, $P = 0.0002$).

1965 and 1991–1996, from 0.385 to 0.152, while the average breeding ratio (the number of successful breeders relative to the number of potential breeders) has declined by nearly half from 0.291 to 0.163 between these two time periods. This equates to some 530 parents producing 675 young annually in the early years, while in the later years, with the population on average 6 times larger, 2500 parents were producing 2300 young each year. This linear relationship is illustrated in Fig. 4, along with the demographic changes the population has exhibited. The consequences of these declines in fecundity measures are highlighted by the *increasing* slope of the ratio of *potential breeders* to lagged population size, and the strongly *decreasing* slope of the trend in the ratio of *actual breeders* to lagged population size. In other words, currently, fewer and fewer birds which could potentially breed actually do so, and of these which breed, their fecundity is lower (e.g. reduced brood-size, etc.). However, the net result, because of the strengths of the relative declines in fecundity measures while the actual number of successful breeders has increased, is that the number of juveniles entering the population each year is increasing. At the same time, survival has been slowly (but significantly) increasing.

Detecting density-dependence and its role in the dynamics of the population

Discussion

Owen & Norderhaug (1977) and Owen (1984) have reviewed the first twenty-odd years of count data, particularly in relation to the growth of the population in relation to various conservation measures taken between the 1950s and early 1970s (see Introduction). In addition, based on the strength of observed density-dependent declines in fecundity, Owen (1984) suggested that the population would level off at around 13,500 birds. The population is currently in excess of 23,000 birds.

How has this population expansion occurred? In terms of demography, all measures of fecundity have declined over the study period, although there is evidence that these declines have begun to level off post-1980. In terms of the actual dynamics of the population's growth, annual productivity has decreased two-and-a-half-fold between 1958–

One traditional way of determining density-dependent limitation in population size is to regress $\ln(N_{t+1})$ against N_t . More useful is to regress the intrinsic growth of the population ($\ln(N_{t+1}/N_t)$) against $\ln(N_t)$. Alone, this tends to over-represent density-dependence, hence the development of alternative techniques based on this ecological principal. Using the conservative method of Pollard et al. (1987), density-dependence in the growth of the Svalbard barnacle goose population could not be statistically detected. However, such statistical detection depends upon a relatively smooth decline in the growth rate ($\ln(N_{t+1}/N_t)$) of the population. Even given the characteristic inter-year variability inherent in birds breeding in arctic and sub-arctic regions, the Svalbard barnacle goose population seems to exhibit distinct 'phases' in its growth, making detection of density-dependent processes more difficult in this population, since potential density-

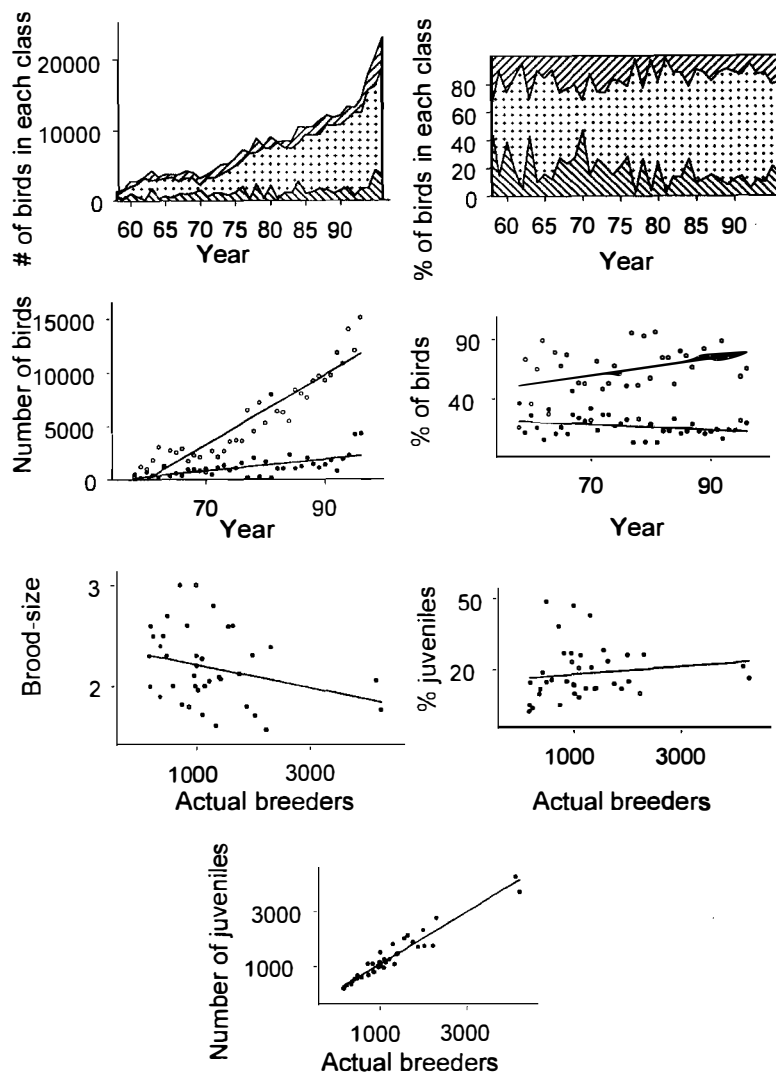


Fig. 4. Changes in the demographic structure of the Svalbard goose population over time. The top two left-hand plots refer to actual numbers of birds and the top two right-hand plots to their respective percentage composition. In the upper graphs, the lower hatched panel refers to juveniles, the second, dotted panel to non-breeding adults, and the third (upper), hatched panel to successfully breeding adults. The lower two graphs of the upper four refer to non-breeders (open circles, dotted line) and successful breeders (solid circles and line). The lower three graphs in the figure examine the relationship between fecundity measures and the actual numbers of successfully breeding adults in each year.

dependent processes are not occurring consistently across the time-frame examined here. However, the significant declines in fecundity measures with increasing population size are indicative of density-dependent limitation of productivity, with high average values at the beginning of the study and through the 1960s, a marked decline in the 1970s, and a leveling off at lower mean values in the 1980s and through the early and mid 1990s. The most recent season's data (1997/98) are consistent with these declines in fecundity now beginning to plateau off. On the other hand,

survival values, as determined from the census data, have been increasing, even after the various conservation measures began to be effective throughout the annual cycle and in all areas.

Thus our interpretation of the demographic processes behind the dynamics of this population can be summarised in terms of the 'phases' of population growth: (i) 1958–1963: the population increases as early conservation measures begin to become effective, with probably higher productivity, but especially a much higher survival rate; (ii) 1964–1970: illegal hunting continues, resulting in

mortality and productivity being in equilibrium; (iii) 1971–1980: creation of additional reserves and further protection from hunting, resulting in higher survival of both juveniles and adults; (iv) 1981–1992: mortality and productivity again in equilibrium, brought about through density-dependent limitation of productivity, in that slopes of productivity against lag population size are still less than one; (v) post-1993: range expansion through-out annual cycle and consolidation of new colonies allowing release from constraints on productivity and further population growth.

Owen & Norderhaug (1977) and Owen (1984) have already documented (i)–(iii) above. Pettifor et al. (1995) used the detailed ringing data of individual birds to assess the strength of the density-dependent processes operating on productivity and survival between 1973 and 1990, a period almost coincident with (iii) and (iv) above. A stochastic age-structured matrix model using these parameter estimates suggested the population leveling off at around 13,000; however, we now know that population sizes were underestimated in the later years of the study and consequently the strength of the density-dependence was overestimated. In addition, we had not taken account of new colonies being formed, about which we have very little information. The importance of density-dependence is illustrated in Fig. 5. We have used three hypothetical breeding colonies, choosing productivity and survival parameters within the range observed at known colonies on Svalbard; we also derived 'idealised' density-dependent functions for these parameters from the observed colony data. In addition, we explored briefly the possible behaviour of the population when the colonies are not able to grow beyond a certain size. The message from these plots is clear. Small differences in the strength of the density-dependence can radically alter equilibrium population size. Thus, if we are to make any attempt to understand the dynamics of the population, we need to accurately estimate density-dependence for all sub-populations of the Svalbard barnacle goose. In addition, all such attempts will be made considerably more difficult because of the exploratory nature of the birds, which results in both new breeding colonies and general range expansion throughout their annual cycle.

The mechanisms behind range expansion and colony development are likely to give rise to the step-wise growth pattern seen in this population

(Fig. 1). The geese are continually expanding their winter range, spending an increasing amount of time in haunts that were once used only at the end of the season (e.g. Southernness and Rockcliffe Marsh, Owen et al. 1987; Black 1998a). This new behaviour was heightened in the late 1980s when the population numbered around 12,000, and it was also illustrated during the current (1997/98) season, when significant numbers were recorded using the Cumbrian side of the Solway for the first time (D. Patterson unpubl.).

The spring staging range has also increased two-fold as an increasing number of birds utilise islands further to the west and north (Black 1998a; Prop et al. 1998). The spring expansion is driven by two main phenomena. There has been a change in coastal/agricultural policies which enhances new sites and allows others to become degraded. In 1989 a major shift occurred away from traditional habitats that had become degraded, to agricultural habitat that was of higher quality. The birds using the new habitat gained more fat reserves more quickly and bred substantially better than those in the old habitats (Black et al. 1991; but see Prop & Black 1998, this volume). There has also been a gradual increase in spring temperatures on Helgeland which has apparently moved the initial spring flush of grasses forward in the more northerly locations, enabling the geese to make use of a hitherto unavailable habitat (Prop et al. 1998).

During the study period, there has also been a large increase in the number and size of colonies in Svalbard, from ten in the 1960s to over 37 in the 1980s, when the last extensive surveys were made (Prestrud et al. 1989). In addition, the number of nests in some older colonies has doubled between 1989 and 1995 (Drent et al. 1998, this volume). Loonen (1997) describes how the recent Kongsfjord sub-population was in existence for 10 years before the first 15 nests were established, and it took 15 years before there were enough breeders in this sub-population to contribute more than 50 goslings to the overall population recruitment (Black & Pettifor unpubl. data). This colony began to contribute at this level in 1991 when other colonies had peaked in productivity, thus contributing to a further phase of increasing numbers until it apparently reached its carrying capacity in 1993 (Loonen 1997). We suspect, therefore, that new colonies are formed by non-breeding birds that gradually gain experience of the intricacies of the new location which enables them to breed successfully (see Black 1998b, this volume).

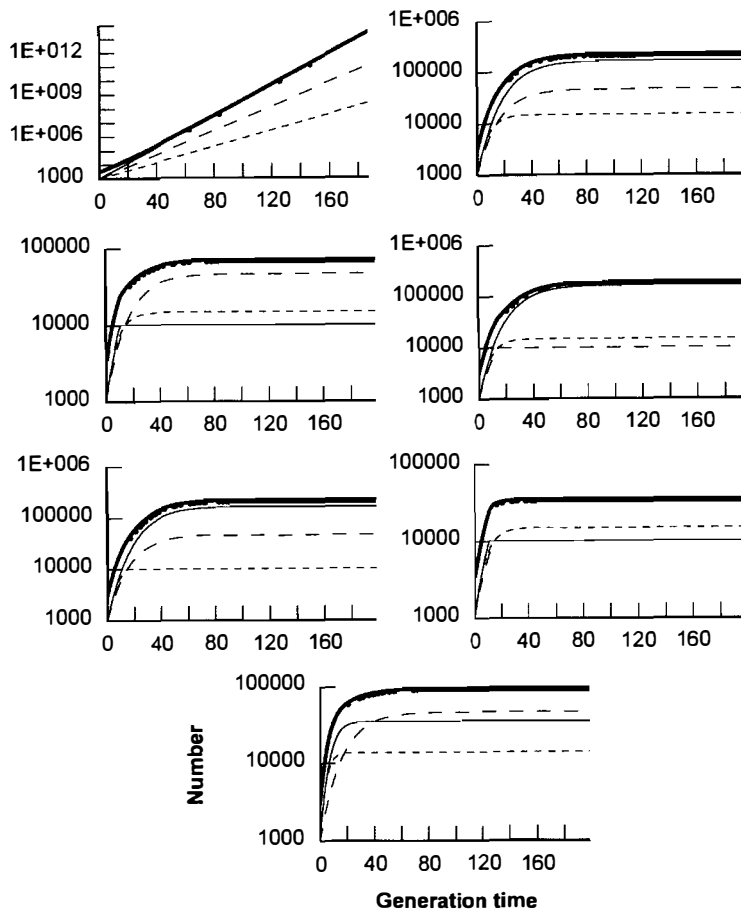


Fig. 5. Hypothetical simulations of population growth stemming from three sub-groups, representing breeding colonies 1, 2 and 3. Both survival and productivity estimates may or may not be density-dependent, and breeding colonies may or may not be restricted to a maximum size (when restricted, then to 10,000 breeding adults in all instances). The hypothetical parameter estimates roughly accord with known values derived from the ringing data: mean reproductive output of the three colonies in the absence of density-dependence was: Colony 1, 0.20; Colony 2, 0.25; Colony 3, 0.30, and density independent survival set at 0.9 for all birds. Density-dependence in productivity was calculated as Colony 1:

Productivity = $1.919 + (-0.1818 \times \ln(N_{t-1}))$; Colony 3: Productivity = $1.957 + (-0.1715 \times \ln(N_{t-1}))$; while productivity was density independent with a mean output of 0.25 at Colony 2 (thus representing hypothetical 'new' colonies). Density-dependent survival was calculated with slopes of $-0.1305 \times \ln(N_{t-1})$, $-0.06454 \times \ln(N_{t-1})$, $-0.05859 \times \ln(N_{t-1})$ for colonies 1, 2 and 3 respectively. The heavy upper line represents total population size, the dotted line Colony 1, the broken line Colony 2 and the lighter continuous line Colony 3. The simulations running left to right down the page were:

Simulation	Productivity	Colony size limited	Survival
1	No dd	No limit	No dd
2	No dd	No limit	All dd
3	No dd	Col 3 limited	All dd
4	No dd	Col 2 limited	All dd
5	No dd	Col 1 limited	All dd
6	No dd	Cols 2 & 3 limited	All dd
7	Cols 1 & 3 dd	No limit	All dd

When the new colonies 'kick in' they may initially contribute disproportionately to the recruitment in the population until local densities exceed local resources (also see Larsson & Forslund 1994). When high densities are reached competition for limited food increases and this influences gosling growth rate (Loonen 1997), ultimate body size (Black *et al.* 1998, this volume), and gosling and female survival (Loonen *et al.* 1998, this volume).

In conclusion, this review emphasises that gross population surveys are no longer sufficient for understanding the demographic changes affecting the dynamics of the Svalbard barnacle goose population. While, on average, fecundity has declined over time, analyses of the detailed ringing data indicate that various factors result in segments of the population being out of phase with one another. Attention needs to be directed at docu-

menting and analysing the behaviour of known individuals using different colonies, wintering areas and staging sites, in order to understand the functional processes driving these differences. Co-ordination and collaboration between all those studying these birds is the only way we can resolve the old paradox that as we learn more about these birds, so more and more questions need answering. Specifically, effort needs to be concentrated on (1) increasing the number of ringed birds in the population, so that these are truly a random sample of the total population; (2) directing the collaborative research effort towards understanding density-dependent processes on the breeding grounds, specifically at a colony level; (3) developing alternative approaches regarding our understanding of this population, ranging from statistical analyses through to a range of modelling techniques (stochastic matrix models & associated sensitivity/elasticity analyses in order to determine key demographic features; stochastic dynamic programming, in order to explore (and test) decision rules; further development of our game-theoretic approach, particularly with respect to the black box still operative in our models regarding the breeding grounds; and finally (4) compiling of sorely needed quantitative data on tradition in geese.

Acknowledgements. – We dedicate this paper to our colleagues in The Netherlands, Norway and the previous and current staff at Caerlaverock and Scottish Natural Heritage who contributed to the success of the Barnacle Goose project over the study period. R. A. Pettifor and J. M. Rowcliffe were supported by NERC grants (GST/02/1202 + 2078). D. Patterson receives core-funding from WWT.

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Behaviour and energetics of Svalbard barnacle geese during their autumn migration

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If the autumn migration of the Svalbard population of barnacle geese consists of 30–40 h of non-stop flying from Bjørnøya (Bear Island) to Caerlaverock, southern Scotland, as suggested by Owen & Gullestad (1984), even the adults, let alone the juveniles, may be close to exhausting the fat stores that they deposit before departing from Svalbard. To determine their behaviour before and during their autumn migration, we attached lightweight satellite transmitters (PTTs) to geese during the summers of 1994 and 1995, and, to obtain some indication of their energy expenditure during this migration, we implanted small heart rate data loggers into the abdominal cavity of others during 1995. The data indicate that most, but not all, of the Ny-Ålesund geese stopped off at Bjørnøya, but none flew non-stop to southern Scotland. The geese all flew along the Norwegian coast, stopping periodically and with non-stop flight duration of on average 13 h. The average total flight time from their departure from Ny-Ålesund to their arrival at Caerlaverock was 61 h. The average heart rate of the geese during migration was 253 beats min^{-1} , which is 50% of that recorded from geese flying behind a truck and 66% of that recorded from geese flying in a wind tunnel. The heart rate data suggest that the energy cost of migratory flight is somewhat less than that recorded from birds flying in a wind tunnel. Depending on the oxygen-carrying capacity of the blood and on the ability of the tissues to extract oxygen, it is tentatively suggested that the average minimum rate of oxygen consumption during migration for a 2.4 kg barnacle goose is somewhere between 170 and 250 ml min^{-1} .

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Introduction

As a result of intensive ringing studies, observations of migrating geese and departure and arrival times from Bjørnøya (Bear Island) and the Solway Firth in Scotland, Owen & Gullestad (1984) concluded that there are likely to be two main autumn migration routes for the Svalbard population of barnacle geese *Branta leucopsis*. One of these would be from Spitsbergen or Bjørnøya and along the western coast of Norway. The other would be a non-stop flight from Bjørnøya to the Northern Isles, with most birds flying directly to the Solway, a distance of some 2,400 km. Assuming an air speed of 60–70 km h^{-1} (16.7–19.4 m s^{-1}) and a mixture of tail and headwinds, Owen & Gullestad (1984) predict that the average, non-stop journey from Bjørnøya to the Solway would take 30–40 h. They go on to say that the patterns of departures from Bjørnøya and arrivals at Solway are consistent with 'the journey

being non-stop for most of the birds'. They even suggest that some birds may fly directly from Spitsbergen to Scotland without stopping at Bjørnøya. If either of these proposals is correct, then this migration is very impressive, especially considering that juveniles of approximately 12 weeks of age also successfully attempt the journey.

Are such journeys feasible in terms of what we know about the energy requirements of forward-flapping flight in birds and are the fat stores of premigratory geese sufficient to meet these requirements for flight durations of 30–40 h? Data from seven species of birds flying in wind tunnels (Butler 1991) and recalculated using reduced major axis regression (Butler & Bishop in press) indicate that the minimum rate of oxygen consumption during forward flapping flight ($\dot{V}\text{O}_{2 \text{ min}}$ in ml min^{-1}) = $160 M_b^{0.74}$, where M_b = body mass in kg. If this relationship is extrapolated beyond the maximum mass (approximately 0.5 kg) of the birds contributing to it, to a bird of 2.4 kg (the mean mass of premigratory,

adult, Svalbard barnacle geese, Bishop et al. 1998), then estimated $\dot{V}O_{2\text{ min}} = 306 \text{ ml min}^{-1}$. This is reasonably consistent with data obtained from barnacle geese flying in a wind generator (P. J. Butler, A. J. Woakes, R. M. Bevan & R. Stephenson, unpubl. data). Assuming that the geese use mainly fatty acids as fuel during their long flights (Butler & Bishop in press; Butler et al. in press), then $1 \text{ ml } O_2 \equiv 19.6 \text{ J}$. Thus, for 30 and 40 h flights, the total, minimum energy expenditure of a 2.4 kg goose would be 10,796 and 14,394 kJ respectively. As the energy density of lipids is 39.3 kJ g^{-1} (Schmidt-Nielsen 1997), the amount of fat deposits used during such journeys would be 275 g and 366 g respectively. Premigratory, adult, Svalbard barnacle geese have, on average, approximately 188 g of total triglycerides kg^{-1} , (Butler et al. 1998) which is 415 g for a 2.4 kg goose.

Although it would appear that the geese have sufficient fat deposits, even for the longest estimated non-stop flight of 40 h duration, it must be remembered that the value for energy expenditure is a minimum estimate. On the other hand, the premigratory geese studied by Butler et al. (in press) were probably captured a few days before they would have departed from Spitsbergen and then would, most likely, have spent a few days on Bjørnøya before setting off for Scotland. They may well have been heavier and possessed more fat than the values given above, although this would probably be more than compensated by the loss in body mass during the migration. It would appear, then, that these birds could be performing at close to the limits of their fuel deposits. It was therefore decided to determine the route that the barnacle geese take during their autumn migration by using the latest, lightweight satellite transmitters (PTTs) and to attempt to obtain some indication of their energy expenditure by continually recording heart rate during migration by way of an implanted data logger (Woakes et al. 1995). It may then be possible to convert heart rate into $\dot{V}O_2$ from data obtained from geese flying in a wind tunnel. This paper presents a preliminary analysis of some of the data from this study.

Materials and methods

Data were obtained from adult barnacle geese of

the breeding population at Ny-Ålesund (79°N , 12°E), which is situated on the western coast of the island of Spitsbergen. Ny-Ålesund is an old coal mining town which now accommodates a number of national research facilities, including those of the Norwegian Polar Institute and the Natural Environment Research Council of the UK. Non-flying birds were captured in corral nets during the postbreeding moult, between approximately the last two weeks in July and the first week in August, in 1994 and 1995. Miniature satellite transmitters (Microwave Telemetry Inc, USA), which weigh 33 g, including the harness, were attached to non-breeders (two females and four males) in 1994. In 1995, a further six birds were equipped with PTTs, but in addition, their partners were implanted with data loggers, which weigh 20 g (Woakes et al. 1995), as were six successful breeders.

The PTT was attached using a harness constructed from soft braided nylon cord (2 mm diam.) with the bird under general anaesthesia (2–3% halothane in 75% air:25% O_2). It was thus possible to ensure that the PTT was correctly fitted and to reduce the stress to the bird. The PTT was mounted on the back, with one loop of cord positioned around the body in front of the wings and a second loop behind them. These loops were buried in the feathers and adjusted to allow three fingers to be just slipped flat between the PTT and the back of the bird. This was estimated to give sufficient room for the growth of the flight muscles that occurs before migration (Bishop et al. 1996). The loops were pulled together under the bird by a short (7–10 cm) length of cord running along the sternum, and all joints and knots were then sealed with cyanoacrylate adhesive. After recovery and release, the bird quickly preened its contour feathers over the PTT, leaving only the short antenna visible. Birds captured the following years (ranging in number from 2 to 4) showed no indication of any damage to the feathers or skin caused by the harness, and there was negligible wear on the harness. Slight feather wear was, however, noticeable under the PTT package itself. Details of the duty cycle of the PTTs and of their accuracy are given in Woakes & Butler (in press).

Briefly, the PTTs can operate continuously for 30 days, but in 1994 a low duty cycle was used initially (6 h on, 250 h off) and a higher duty cycle was used when the birds were estimated to begin moving south from Ny-Ålesund (4 h on, 12 h off). Continuous transmissions were then used just before the migration was expected to start.

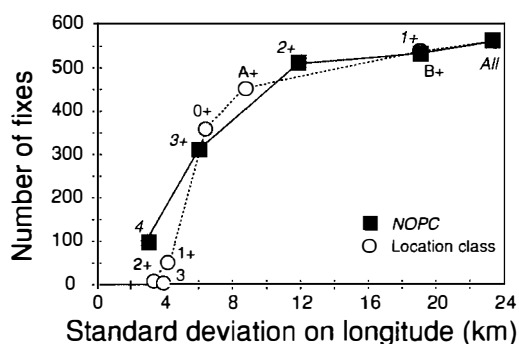


Fig. 1. The standard deviation on longitude of sub-groups of the satellite fixes from barnacle geese equipped with PTTs on Bjørnøya in 1994, plotted against the number of fixes in that group. Each point represents a group of fixes which all have the Quality Indicator values shown (e.g. the point 2+ is the group with NOPC values of 2, 3 and 4). See text for further information. (Woakes & Butler in press)

Unfortunately, the estimated start of the migratory period was incorrect for that year and only 2 birds gave continuous fixes during the migration, the others were on the 4:12 h duty cycle. It was noticed, however, that during flight the temperature of the PTTs (transmitted as part of the data) dropped considerably, so for the succeeding season the timer was modified to trigger transmission from the internal temperature sensor.

System Argos provides limited information on the likely accuracy of any fix (Service Argos, 1996). All fixes include two indicators of the location reliability, Location Class (LC) and Number of Successful Plausibility Checks (NOPC). In order of increasing reliability, LC is indicated by the symbols B, A, 0, 1, 2, 3 and NOPC by 0 through 4. The actual accuracy of the fix is only given to data with an LC of better than class 0. Little or no data are given for classes 0, A or B, which make up the majority of fixes in this type of application, or for the alternative non-parametric index, NOPC. Thus, the accuracy of the fixes supplied by System Argos was assessed by utilising the fact that some of the birds spent a few days on Bjørnøya, which is 15×20 km. Although the absolute position of the birds on the island was not known, it was assumed that their position had a normal distribution, with an associated standard deviation (SD), and any error in the fix would increase this SD. The fixes were, therefore, sorted into subgroups on the basis of (a) the two values of the quality indications (QI) supplied with each fix,

LC and NOPC, and (b) by excluding fixes poorer than the particular value of the QI under consideration. The SD of the position in longitude (as this is the smaller dimension of the island) was then calculated for each subgroup. The SD of all 553 fixes is 23.4 km. As poorer classes (starting with class A for LC and class 0 for NOPC) are eliminated, the SD eventually drops to about 3 km for both quality indices, but with a far higher number of remaining fixes for NOPC (105 of value 4) than for LC (13 of value 2 and higher, Fig. 1).

While no figures can be given for the absolute accuracy of these selection methods, it is probable that the underlying distribution of the birds themselves is represented by the lowest SD, of about 3 km, with any additional error due to the inaccuracy of the system. It must also be remembered that this analysis is in one dimension only and that error in latitude will increase the inaccuracy (analysis on latitude gives very similar figures to those presented here for longitude). Fixes with NOPC of 2 and higher were used for tracking migration in the present study. Although they have a probable error (SD) of 12 km on longitude, this is negligible compared with the distances flown.

The implantation procedure for the data loggers was essentially the same as that used to implant ECG transmitters (Stephenson et al. 1986). Briefly, the birds were anaesthetised with halothane (see above). The incision area was washed with a chlorhexidine solution, which also served to deflect the feathers. The sterilised data logger was implanted into the abdominal cavity via mid-line incisions in the skin and body wall. Suture thread tied around the body of the data logger was used to anchor it in place. Chromic catgut was used to suture the body wall muscle and thread was used to suture the skin. An antibiotic powder was dusted into the wound area and a long acting antibiotic (Terramycin LA, Pfizer) injected intramuscularly. The time at which the logger was implanted was accurately noted. The loggers were programmed with an initial delay of 15 days and then to record heart rate every min and temperature every 4 min. This gave a logging period of 72 days.

All the birds had a yellow or green numbered ring on one leg, but to aid recapture the following year (for details, see above), a red ring was fitted to the other leg. Recapture success was approximately 55%, and upon recapture the data logger was removed using the same procedure as during implantation (see above) and the data were

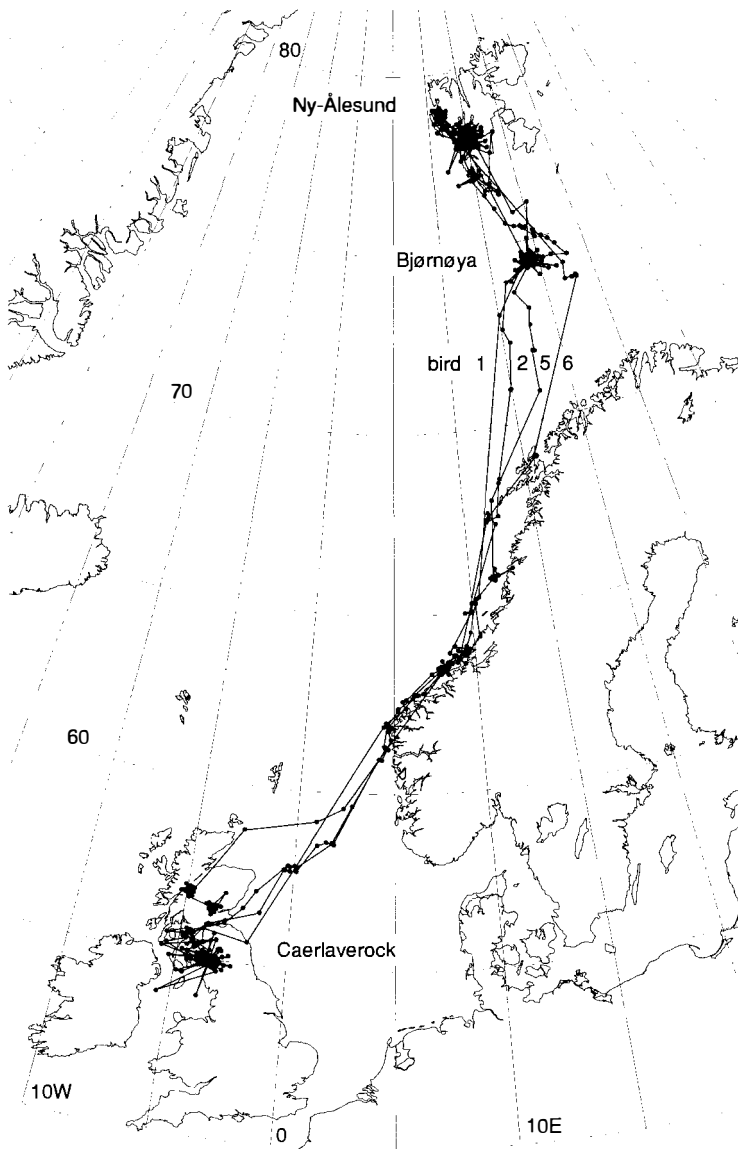


Fig. 2. Complete tracks obtained from satellite transmitters (PTTs) attached to 4 barnacle geese migrating from Ny-Ålesund to southern Scotland in 1994. The sex and mass of the birds at the time of attachment of the PTTs were: bird 1, female and 1.56 kg; bird 2, female and 1.38 kg; bird 5, male and 1.54 kg; bird 6, male and 2.07 kg.

downloaded for further analysis (see Bevan et al. 1995 for details). Mean values are given \pm SE of the mean.

Results

Migration route

The complete tracks for four of the geese (there

were incomplete tracks for the other two birds) in 1994 are shown in Fig. 2. All six birds left Ny-Ålesund around the end of August and spent about 3 weeks at a latitude of 78°N and at longitudes between 14.5° and 16.0°E . This is a region of valleys, south of Longyearbyen and Barentsburg. The birds then travelled directly to Bjørnøya, although two of them did not stop at the island (only one of these is shown in Fig. 2), as was also the case in 1995, but flew directly to Norway. The birds on Bjørnøya spent between 4–12 days there, mainly in the southern part, before following the

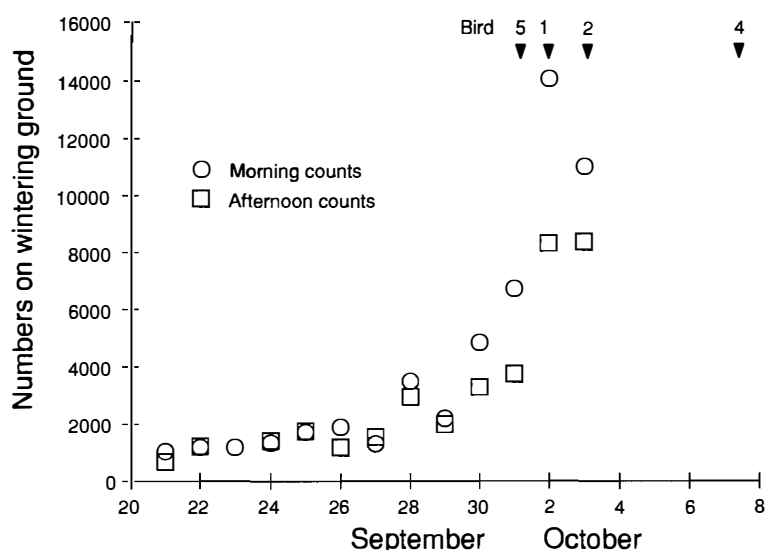


Fig. 3. The numbers of barnacle geese at the Wildfowl and Wetlands Trust refuge at Caerlaverock during the last few days of September and the beginning of October in 1994 (\square morning counts, \circ afternoon counts, data supplied by J. M. Black) and the arrival dates of those birds with satellite transmitters (PTTs) attached to them. Bird 6 arrived on 1 November and bird 3 on 9 November. Sex and mass of the birds at the time of attachment of the PTTs were: birds 1, 2, 5 and 6, as for Fig 2; bird 3, male and 1.72 kg; bird 4, male and 1.86 kg.

Norwegian coast en route for Scotland. The coastal route was also taken by all of the birds in 1995 (Woakes & Butler in press). In 1994, three of the birds arrived at Caerlaverock during the latter half of the population build-up on the wintering grounds (Fig. 3), while two spent some time on Tayside (4 and 28 days) before joining the main flock. In 1995, a long period of southerly winds delayed the birds from crossing from southern Norway to Scotland and they arrived some 10 days (three birds) and 24 days (two birds) later than the build-up of the majority of the birds for that year.

From the heart rate data, it is clear that the geese did not fly continuously from Bjørnøya to Scotland and that they stopped periodically (Fig. 4), probably while travelling along the Norwegian coast. This was the case, whether or not they had a partner carrying a PTT. Fig. 5 shows both positional data from a male carrying a PTT and heart rate data from its partner which had a data logger implanted. The following comments are made on the assumption that this pair of geese flew together. For the fixes obtained on 7 and 9 October 1995, the straight line route between them is across the Norwegian Sea. From the heart rate data, there seem to have been three flights of a few hours duration, with periods of non-flying in between. This would tend to indicate that the birds landed on the sea, if they did not go via the Shetland Islands. A clearer example can be seen on the night of 2 October, when several fixes were obtained when the birds were out at sea, yet not flying.

It is also possible from the heart rate data to determine the total flying time during the migratory period, from the end of August, when the geese left Ny-Ålesund and until they arrived in Caerlaverock. For four geese in 1995, the total duration of all flights longer than 15 min was 61.2 ± 2.3 h. For the same four birds, the mean duration of the longest, non-stop flight was 13.1 ± 0.5 h and the average number of flights of longer than 1 h duration was 11.5 ± 0.6 . Two of these birds were non-breeders, whose partners carried PTTs, and two were breeders, whose partners did not have PTTs. The mean duration of all flights was 63.2 h for the non-breeders and 59.2 h for the breeders. Mean duration of the longest flights was 12.35 h and 13.58 h, respectively.

Heart rate and the energetics of migration

There was a clear diurnal rhythm in heart rate from approximately 10 August with the magnitude of the oscillation increasing as the migratory period approached (Fig. 6). There were also noticeable decreases in both the mean daytime heart rate and the hourly mean minimum night-time rate. It is also clear from Fig. 6 that the mean daily heart rate during flight was, for this bird (the same one as in Fig. 4) no higher than $300 \text{ beats min}^{-1}$ and that it decreased on successive days of the migration

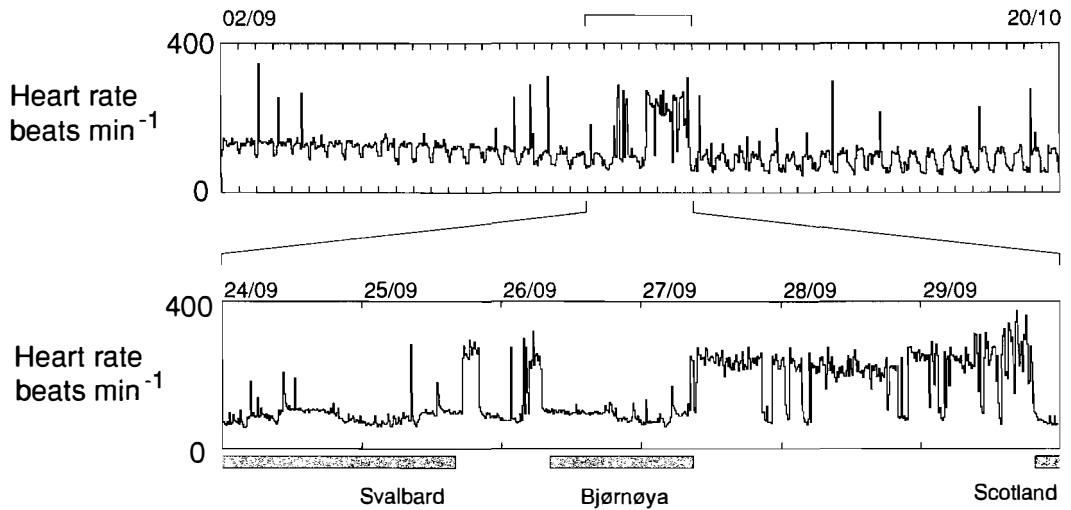


Fig. 4. The top trace is a continuous record of heart rate obtained from a male barnacle goose between 2 September and 20 October 1995. This bird had a mass of 1.98 kg at the time of implantation of the data logger and was one of a pair of failed breeders. Note the daily rhythm in heart rate when the bird was not flying. The lower values are during the night hours (i.e. around midnight). The lower trace is an expansion of the above between the dates of 24 and 29 September, which covers the period of migration from Ny-Ålesund to southern Scotland.

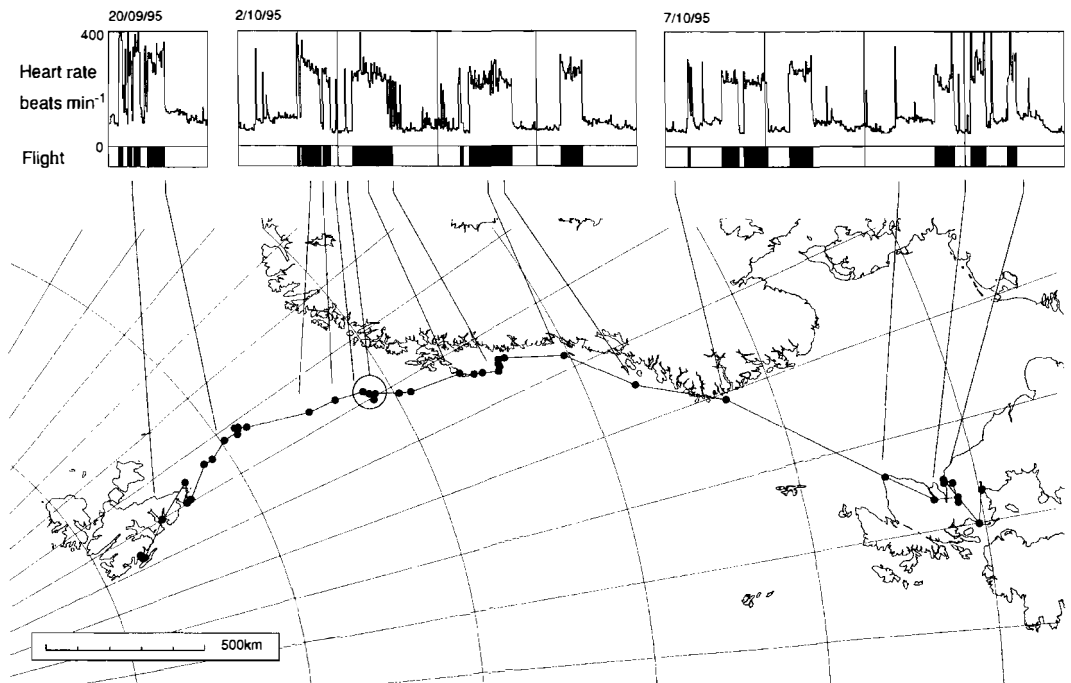


Fig. 5. Satellite track and heart rate data from a pair of non-breeding barnacle geese during their autumn migrations in 1995. It is assumed that they travelled together. The bird from which the satellite track was obtained was a male and had a mass of 2.09 kg when the satellite transmitter was attached. The other bird was a female with a mass of 1.64 kg when the data logger was implanted. Some fixes are circled which corresponded to times when the birds were not flying and yet when they were out at sea.

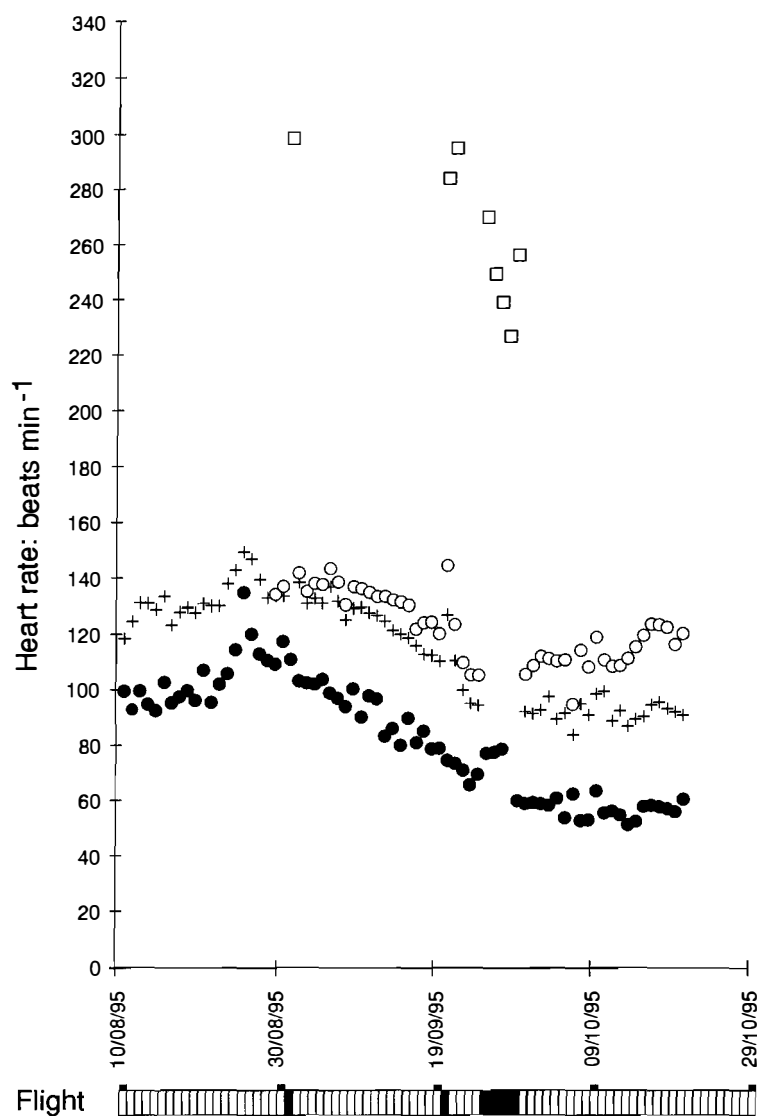


Fig. 6. Mean heart rate data from a male barnacle goose (1.98 kg at time of implantation of data logger) from 10 August until 21 October 1995 (see Fig. 4). ● Mean minimum daily heart rate (hourly mean), + mean daily heart rate, ○ mean heart rate during the daylight hours, □ mean daily heart rate during flight.

from 298 to 226 beats min^{-1} (which is probably related to a reduction in body mass), until the last day when it increased to 256 beats min^{-1} . Mean heart rate during all migratory flights for the two non-breeders and two breeders referred to above was 253 ± 9.5 beats min^{-1} . This is 50% of that obtained from two barnacle geese flying behind a truck for an average of 14.4 min and at air speeds between 15 and 22 m s^{-1} (Butler & Woakes 1980) and 66% of that obtained from three barnacle geese flying in a wind generator for an average of

7.9 min and at approximately 11 m s^{-1} (P. J. Butler, A. J. Woakes, R. M. Bevan & R. Stephenson, unpubl. data, Fig. 7). We also have values for $\dot{V}\text{O}_2$ obtained from the geese flying in the wind tunnel (P. J. Butler, A. J. Woakes, R. M. Bevan & R. Stephenson, unpubl. data) but, because of the large difference in heart rate between the migrating geese and those flying in the wind generator, it is doubtful if these values of $\dot{V}\text{O}_2$ bear any relationship to those of migrating geese.

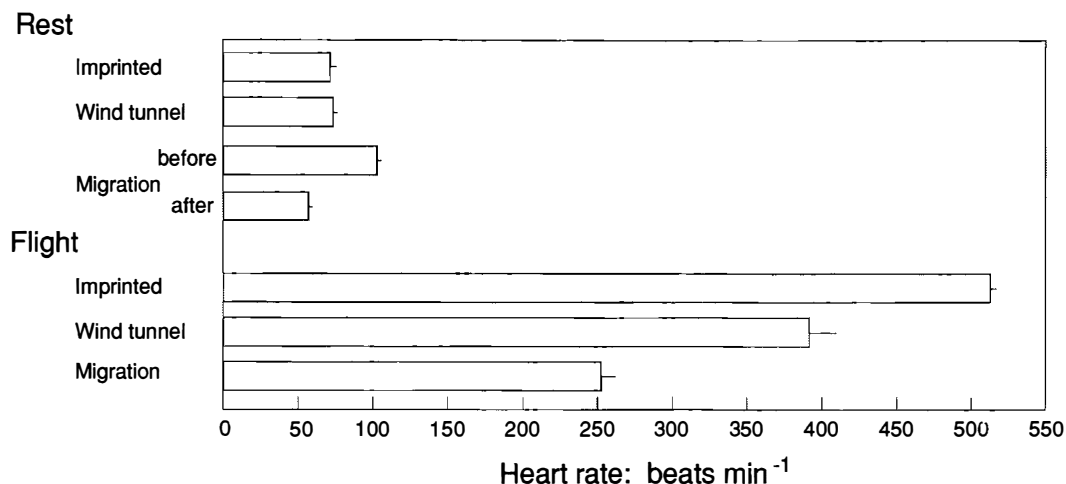


Fig. 7. Histograms of mean (\pm SE) resting heart rates and mean (\pm SE) heart rates during flight of 2 imprinted barnacle geese (mean mass, 1.6 kg) flying behind a truck (Butler & Woakes 1980), of 3 barnacle geese (mean mass, 1.68 kg) flying in a wind generator (P. J. Butler, A. J. Woakes, R. M. Bevan & Stephenson, unpubl. data) and of 4 barnacle geese (mean mass 1.92 kg at time of implantation of data loggers) during their autumn migration.

Discussion

A question mark can always be raised against data obtained from animals wearing externally mounted equipment. This is especially true when the animals are swimming, running or flying, when the drag of the equipment could affect their performance. It has been noted, however, that the effect may be minimal for a relatively small device that the bird can preen under its feathers (Obrecht et al. 1988), which is exactly what the geese did in the present study. In 1994, three of the birds arrived in Caerlaverock within the same period as the majority of the population. The fact that these birds arrived toward the end of the period may not be too surprising, as the Ny-Ålesund geese are at the northern limit of the main breeding area in Svalbard (Mehlum 1998, this volume) and little is known of the timing of their migration relative to that of the population as a whole. However, in 1998 'many' barnacle geese were observed resting on an island outside Kristiansund (approximately 63°N) during the last week of September (A. Follstad, pers. comm.), whereas 32 geese were observed just outside Tromsø (approximately 69.5°N) on 12 October (G. W. Gabrielsen, pers. comm.). Among the latter group were two birds with red rings, i.e. they were from the Ny-Ålesund population.

There have also been some very late arrivals in Caerlaverock during the last few years, with groups of geese being seen in many places within the United Kingdom after their journey from the coast of Norway (Madsen et al. 1998, this volume). Strong southerly winds, as occurred in 1995, could contribute to the late arrival of some geese in Caerlaverock. The fact that a number of the geese with PTTs were also seen in Ny-Ålesund the following year, indicates that the PTTs were not preventing successful migration in at least 50% of the birds. This is similar to the percentage recovery of the birds with implanted data loggers. Although we cannot exclude the possibility that the PTTs have some adverse effects on the geese, there is no reason to believe that they are excessive.

The present study indicates that, at least for the Ny-Ålesund population, barnacle geese do not fly non-stop to Scotland, either from Spitsbergen or from Bjørnøya, although not all of the birds seem to stop off at Bjørnøya, all of those with PTTs did fly along the Norwegian coast. In addition, all of those with data loggers, whether or not their partners were equipped with a PTT, did not fly for longer than an average of 13 h without stopping. If their ground speed was around 70 km h⁻¹, they would have covered approximately 1000 km during such a flight. Whether they stopped because of loss of navigational cues, in order to feed, drink, wait for favourable winds or merely for a rest, is

not known. However, it is only likely to have been to rest, because of a loss of navigational cues or to avoid unfavourable headwinds when they landed on the sea, which they seemed to on occasion. Thus, these birds appear to perform flights that alone are not sufficient to reduce their fuel stores close to exhaustion.

The heart rates recorded from the migrating geese are only a fraction of those recorded from imprinted geese flying behind a truck (Butler & Woakes 1980) and from those flying in a wind tunnel (P. J. Butler, A. J. Woakes & R. Stephenson, unpubl. data). However, they are similar to the heart rates recorded from the imprinted geese when they occasionally slope-oared over the top of the truck containing their foster parent (Butler & Woakes 1980). The fact that resting heart rates are similar for the wild geese and for those trained to fly behind a truck and in a wind tunnel (Fig. 7) indicates that the data from the logger are accurate. As such, it would not be justified to use the values of $\dot{V}O_2$ obtained directly from barnacle geese flying in a wind tunnel in order to estimate the energy cost of migration of barnacle geese.

There are three possible explanations for the relatively low heart rates during migratory flight:

(1) Bishop et al. (1998) reported that heart mass of premigratory adult geese was some 17% greater than that in captive geese and 24% greater than that of wild postmoult geese. Thus, for a given $\dot{V}O_2$, heart rate could be lower in wild, premigratory geese than in captive geese, or even than in postmoult wild geese. Certainly resting heart rate decreases in wild birds during the period leading up to migration (Fig. 6), when worsening weather conditions might be expected to lead to a rise in metabolic requirements.

(2) Inter-species heart rate during flight is negatively related to body mass (M_b) ($M_b^{-0.19}$, Bishop & Butler 1995). Although it is not clear whether the same relationship exists for intra-species scaling, it is clear that the premigratory birds are much larger than the other barnacle geese that have been studied.

(3) The energy cost of flight during migration in these birds is much lower than has been suggested from data obtained from birds flying in wind tunnels, possibly as a result of formation flight (Lissaman & Scholenberger 1970; Hummel 1995). Thus, if a captive goose weighing 1 kg has a heart rate of 381 beats min^{-1} when flying in a wind generator (Fig. 7), a migrating goose weighing

2.4 kg would, on the basis of (1) and (2) above, be expected to have a heart rate of 305 beats min^{-1} , which is some 50 beats min^{-1} greater than that actually recorded from migrating geese. This suggests that the energy cost of migratory flight is somewhat lower than that of flying in a wind tunnel.

Without some idea of the relationship between heart rate and $\dot{V}O_2$ during migratory flight, or during conditions that simulate those during migratory flight, the above approach is not that helpful. However, using the equation from Bishop & Butler (1995), where $\dot{V}O_2$ during flight = heart rate \times cardiac stroke volume \times 0.083, cardiac stroke volume during flight = 0.3 (heart mass)^{1.05} and the value for heart mass in premigratory, adult geese = 0.83% body mass \times 1.15 (Bishop & Butler 1995; Bishop et al. 1998), then average minimum $\dot{V}O_2$ during migratory flight for a 2.4 kg barnacle goose would be: $253 \times 8.04 \times 0.083 = 169 \text{ ml min}^{-1}$. The value 0.083 is based on the difference in the oxygen content in arterial and mixed venous blood ($C_aO_2 - C_vO_2$) of pigeons flying in a wind tunnel (Butler et al. 1977). If this value is assumed to be correct for all the flying that is performed during the migratory period by barnacle geese, then a 2.4 kg goose would use 308 g of fat during 61 h of flying and still have 140 g in reserve (see Introduction).

Although birds appear to have lower values of $C_aO_2 - C_vO_2$ than similar sized mammals, because C_aO_2 is not reduced to such a low level (Butler 1991), migrating geese may extract more oxygen from their arterial blood than the pigeons flying in the wind tunnel. If so, their $\dot{V}O_2$ during migration would be proportionately higher than the value given above. For example, with a haemoglobin concentration of 16.1 g dl^{-1} (Deaton et al. 1998, for captive, adult barnacle geese) and if 1.34 ml O_2 combine with 1 g of haemoglobin, 95% saturated arterial blood would contain 20.5 ml O_2 (dl blood)⁻¹. This is some 5.4 ml O_2 (dl blood)⁻¹ greater than that in the arterial blood of the pigeons (pre-flight) used by Butler et al. (1977), but if the same proportion of O_2 (approximately 60%) is extracted by the tissues, the oxygen extraction factor of 0.083 in the above equation would be substituted with a value of 0.123. In this case, estimated average minimum $\dot{V}O_2$ during migration for a 2.4 kg barnacle goose would be 250 ml min^{-1} , which is equivalent to 456 g of fat during 61 h of flying. Under such circumstances, it would use all the triglyceride reserves determined

for pre-migratory, adult geese by M. Butler et al. (in press). However, it must be remembered that the mass of the bird, and hence its $\dot{V}O_2$, would decrease throughout the migratory period (Butler et al. in press).

There is increasing evidence that protein catabolism is essential during periods of starvation and/or during prolonged periods of exercise (Butler & Bishop in press). As protein stores (e.g. muscles, intestines) are less energy dense than fats (Schmidt-Nielsen 1997), they could be just as limiting as fat stores in long distance migrants such as the barnacle goose (Butler et al. in press).

Although the data presented here have clarified many aspects of the behaviour of the Ny-Ålesund population of barnacle geese before and during their autumn migration, they have raised more questions than they have answered concerning the physiology and energetics of this behaviour. The physical condition of the birds (e.g. fat stores immediately before departure from Svalbard/Bjørnøya, oxygen carrying capacity of their blood, oxygen extraction factor during flight), their flight behaviour (e.g. altitude, formation flight) and prevailing weather conditions are some of the important features about which we need more information before it will be possible to begin to give a full explanation of these data.

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Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats

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Prop, J. & Black, J. M. 1998: Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats. Pp. 175–193 in Mehlum, F., Black, J. M. & Madsen, J. (eds.): Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skriftr 200*.

This paper concerns the effect of habitat choice on the dynamics of deposition of body reserves in spring-staging barnacle geese *Branta leucopsis*. On their way to breeding areas in Spitsbergen, these geese reside for several weeks on islands off the coast of Helgeland, Norway. They use three distinct habitat types: (1) managed islands, which are covered by Hay meadows fringed by salt marsh vegetation and where grazing by livestock occurs; (2) abandoned islands, where in the absence of people the vegetation on the upper parts of the islands has developed towards communities dominated by tall herbs; and (3) agricultural islands, where pastures are the mainstay for the geese. In each of these habitats data were collected on intake and digestibility of food components. Habitat-mediated differences in the birds' foraging performance resulted in large variation in the accumulation rate of fat and protein reserves. Total body reserves deposited by birds on abandoned islands were 11% less than reserves deposited by birds in a managed habitat. Geese on agricultural islands deposited much larger fat reserves than birds in the other habitats, whereas their protein reserves were smaller. Fat deposition rates in the three habitats were related to different levels of digestibility and ingestion rate of the food. The probability of raising offspring through to autumn was positively related to the fat scores that individuals had achieved by the end of the staging period. However, this was not the case for geese staging in agricultural habitat, possibly because the small amounts of protein accumulated may have prevented the development of a sufficiently strong muscle system. Creating reserves on agricultural land to accommodate geese in spring may therefore have negative consequences on the birds' reproductive performance.

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Introduction

Food resources available during the non-breeding season can affect an individual's fitness by influencing its reproductive success (Davies & Cooke 1983; Thomas 1983; Daan et al. 1989). The link between reproductive success and habitat choice outside the breeding season is particularly important in migratory birds that breed at northern latitudes but winter in temperate regions which are often influenced by man. This implies that management of the winter habitat could affect the productivity of the population.

Geese breed in arctic regions and generally winter some thousands of kilometres to the south (Owen 1980). During recent decades many goose

populations have shown a tendency to shift from natural towards man-made habitats (Owen 1980; Robertson & Slack 1995), thus becoming increasingly dependent on agricultural crops. Agricultural foods are highly digestible but contain fewer nutrients than natural vegetations provide. Foraging on food that has a high metabolisable energy content can be costly when the need for required protein is not met (McLandress & Raveling 1981; Madsen 1985; Alisauskas et al. 1988).

In our study of the barnacle goose *Branta leucopsis* population breeding in Spitsbergen, habitat choice and body condition during spring migration and the subsequent reproductive success could be established. This bird is therefore an appropriate subject for studying the relationship between pre-breeding habitat choice and subse-

quent reproductive success. The population used three distinct habitats: (1) Managed islands, where local people keep low densities of cows and sheep; (2) Abandoned islands, which were once inhabited by people; and (3) Agricultural areas, where geese depend largely on pastures managed by dairy farms.

Since the early 1980s goose numbers on managed islands have remained constant, whereas those on abandoned islands decreased (Prop et al. 1998). The agricultural area was discovered by geese in the 1980s (Black et al. 1991). Seven years after the first flocks of geese had been observed on these islands, more than 30% of the whole population used this newly colonised habitat.

Interested in studying the phenomenon and consequence of this habitat change, we posed two questions: (1) What are the implications of habitat choice for the reproductive success of geese? and (2) Could a difference in breeding success explain why geese progressively shifted towards the agricultural habitat?

To find answers to these questions, we based our work on three levels of enquiry: (1) Determining the quality of the habitats in terms of food intake; (2) Estimating the accumulation of body reserves within each of the habitats. Fat and protein reserves were estimated separately by assessing the intake and output of energy and nitrogen. An independent measure of fat reserves (i.e. fatness score) was obtained from abdominal profile indices (Owen 1981); and (3) Investigating the fitness consequences of the amount of body reserves deposited. This was done by comparing the reproductive success of individuals using different habitats.

Study area

Data were collected in the coastal area of Helgeland, Norway (65°45'N, 12°E). Over 10,000 small islands are scattered off the coast, extending up to 40 km from the mainland. Many islands are steep and barren, but islands that are flat and close to sea level usually provide vegetation suitable for geese (Gullestad et al. 1984). Throughout the area, small settlements, where fishermen/farmers and their families live, are located on so-called Home islands. Each of these islands is surrounded by a scatter of Outer islands, together forming a cluster of managed islands.

Home and Outer islands are grazed by sheep and cattle, and the vegetation is cut for hay-making. Typical for managed islands is the presence of Hay meadows, which are characterised by a high density of grasses (mainly *Poa* spp.) attractive to geese. In the 1970s and 1980s many of the local people moved to the mainland, and the traditional management came to an end. Hay meadows are almost lacking on abandoned islands (Prop et al. 1998); the upper parts of these islands are covered by a vegetation predominated by herbs that are inedible to geese. Managed and abandoned islands are fringed by salt marshes that are heavily used by geese. The marsh zones are dominated by *Puccinellia maritima*, *Festuca rubra* and *Agrostis stolonifera*. The agricultural areas are located on larger islands close to the mainland. Main crops grown on the fields are *Phleum* spp. and *Poa* spp. In each of the main habitats, a study island was selected: Sandvær (visited in 1988–1992), Laanan (1987, 1989–1993), and Herøy/Tenna (1988–1993), representing managed, abandoned and agricultural habitat, respectively. The islands of Sandvær and Laanan are within the traditional range of the geese (Gullestad et al. 1984). Most of the observations on Laanan and Sandvær were collected on the Home islands which are visited by geese from dusk to approximately 8 a.m. During the remaining part of the day geese feed on surrounding islands. Data on body condition and the identity of ringed geese were collected in all the years the islands were visited. We included data collected in 1980–1982 on Laanan, which in those years had the characteristics of a managed island (people abandoned the island in 1980). Other data were mainly collected from 1990 through 1993.

Methods

Analyses on plants and droppings

At intervals of 3 days, samples of the main plant species were collected by carefully imitating goose grazing with finger and thumb. Within *Festuca rubra* we made a distinction between two different types. One type dominated most of the *Festuca*-zones along the shores, the other—which we called *Festuca*-low—was more patchily dis-

tributed closer to the shore line. Samples were immediately dried at 70°C and stored for later processing. The amount of material collected varied between 5 and 15 g dry weight per sample. Samples were ground in a mill to pass through a sieve of 1 mm. They were then analysed for total nitrogen (Kjeldahl, modified to include nitrate), acid detergent fibre (ADF, one of the cell wall components, Goering & Van Soest 1970), and ash (by incinerating samples for 8 hours at 500°C in a muffle furnace).

Each day 5–10 samples of 20 droppings were collected. In the agricultural area this was done at intervals of 4 days. Care was taken to collect only fresh droppings by selecting sites where geese had been observed the preceding few hours. Samples were dried at 70°C and stored. Later in a laboratory samples were re-dried to constant weight, and weighed. For further analyses samples collected the same date were pooled (two bags per day), and homogenised in a blender. First, these pooled samples were used to assess diet composition by microscopical analysis. Identification of fragments was based on the form and structure of the epidermal cells (Owen 1975), which allowed to identify separate genus, species or *Festuca*-type. An adequate amount of material was taken to cover most of the surface of a slide. Preparations were non-permanently mounted in water, and no additional procedures were required to improve the identification of fragments. The relative proportions of food components were determined by systematic point sampling (Prop & Deerenberg 1991). Subsequently, the samples were ground in a mill to pass through a sieve of 1 mm, and they were analysed for ash, total nitrogen and ADF. To avoid the complications of nutrients leaching from the droppings, only samples collected under dry conditions were analysed.

Dropping rate

Dropping rates were assessed by following foraging geese and timing the production of consecutive droppings. Only birds within close range (less than 100 m, and most often within 50 m) were followed, and observations on a particular bird were stopped as soon as the abdomen was out of view. By using markers set out by the observers as reference points, in addition to micro-features in the terrain, the exact location of droppings

observed at the time of production was noted. After the geese had left, droppings were recovered and dried for later re-drying and weighing.

Abdomen profile

The abdomen profile (AP; Owen 1981) was used as an index for the amount of body fat deposited. AP's were assessed on a scale from 1 to 7. Consistency in observations between years and habitats was achieved by placing a set of dummy geese with different AP's on the main observation sites as a reference. Only observations on birds that were individually recognisable by leg rings with inscriptions were used. Studies on pink-footed geese *Anser brachyrhynchus* and Hawaiian geese *Branta sandvicensis* showed that AP classes (similar to ours) are linearly related to fat reserves (Madsen et al. unpubl.; Zillich & Black in press). As we assume this holds for barnacle geese as well, we treat AP as an ordinal-scaled variable.

Reproductive success

Parents and their offspring usually stay together for at least 6 months (Black & Owen 1989), and this enabled us to determine the number of goslings that survive up to winter as a measure of reproductive success. Observations in the wintering grounds were collected at Caerlaverock, Scotland. For further analysis, pairs were classified as successful (observed with at least 1 gosling) or unsuccessful (no goslings). Data of geese observed both in spring and in subsequent autumn allowed a comparison between reproductive success and final AP prior to departure for the breeding grounds (i.e. average AP after 14 May, rounded to the nearest integer).

Calculations

Protein content in plants was calculated by multiplying total nitrogen by a factor of 6.25. Apparent digestibility of the food (% on an ash-free basis) was calculated following van Soest (1982):

$$D = 100 \times (1 - M_f/M_d)$$

where M_f and M_d are the concentrations (ash-free) of a marker in the food and droppings, respectively. We used ADF as a marker. As a small proportion of ADF may be digested in spring (Prop & Vulink 1992) estimates of digestibilities are conservative. M_f was calculated from the regressions of ADF in food plants by date, where the relative importance of each species was weighted by the occurrence in the diet.

Ingestion rate of organic matter (g min^{-1}) was calculated as:

$$IR = (W/I) \times (100/(100 - D))$$

where W = average dropping weight (ash-free) of the sample; I = average dropping interval derived from the regression of intervals by date (see Results). The quotient of W and I estimates the egestion rate during foraging, and observations were therefore only collected while geese were active (feeding plus short vigilant spells, as opposed to periods of loafing lasting for at least several minutes).

Digestion rate (g min^{-1}) was calculated as:

$$IRD = IR \times (D/100).$$

Apparent assimilation efficiency of nitrogen (%) was calculated as:

$$AN = 100 \times (1 - (M_f/M_d) \times (N_d/N_f)),$$

where N_f and N_d are the proportions of nitrogen (ash-free) in food and droppings, respectively. N_f was calculated from the regressions of nitrogen in food plants by date, where the relative importance of each species was weighted by the occurrence in the diet.

Ingestion rate of nitrogen (g min^{-1}) was calculated as:

$$IRN = IR \times (N_f/100).$$

Assimilation rate of nitrogen (g min^{-1}) was calculated as:

$$IRAN = IR \times (N_f/100) \times (AN/100).$$

Excretion rate of nitrogen (g min^{-1}) was calculated as:

$$ERN = (W/I) \times (N_d/100).$$

The excretion of nitrogen is a continual process, and we estimated excretion rates during rest (ERN_0) from the regression of ERN on $IRAN$ by extrapolating to a nitrogen ingestion rate of 0.

Accumulation of nitrogen (g day^{-1}) was calculated as the difference between ingested and excreted nitrogen:

$$S_N = (IRAN \times \text{Active}) - ERN_0 \times (24 \times 60 - \text{Active}),$$

where Active is the number of min per day geese were foraging: 990 min in managed, 1044 in abandoned and 888 min in agricultural habitat ($F_{2,340} = 15.38$, $P < 0.005$; data derived from Black et al. (1991), supplemented with data collected on Sandv r and Her y/Tenna in 1990, P. Shimmings, unpubl.).

Accumulation of protein stores (g day^{-1}) was calculated as:

$$S_P = S_N \times 6.25,$$

assuming 16% of protein is composed of nitrogen (Blaxter 1989).

Energy available for accumulating fat stores was calculated as the surplus of metabolisable energy intake after allowing for energy required to maintain body mass and for energy invested in protein stores:

$$PE_{FAT} = (IRD \times EM \times \text{Active}) - DME - (S_P \times E_{prot}/EFF_{prot}).$$

This results in an accumulated amount of fat (g day^{-1}) of $S_{FAT} = (PE_{FAT} \times EFF_{FAT})/E_{FAT}$. EM is an estimate of the energy content of metabolised matter, derived from digestion trials on barnacle geese feeding on different grass species (Prop & Lichtenbelt, unpubl.). This value shows little variation and is taken at 18.6 kJ g^{-1} . Energy content of protein and fat, respectively (Schmidt-Nielsen 1975) are $E_{prot} = 18 \text{ kJ g}^{-1}$ and $E_{fat} = 39.5 \text{ kJ g}^{-1}$. Efficiency of synthesis of protein and fat tissue, respectively (energy retention as a proportion of energy invested; Simon 1989) are $EFF_{prot} = 0.61$ and $EFF_{fat} = 0.77$. The daily metabolisable energy requirement to maintain constant mass DME was estimated at $2 \times \text{BMR}$ (Basal Metabolic Rate according to Aschoff & Pohl (1970)). Body mass was assumed to be similar to the Baltic-Russian barnacle goose population (derived from Ebging et al. 1991: in May increasing from 2.0 to 2.4 kg).

Data were analysed using a standard statistical package (SPSS, Norusis 1993). Diet was analysed by MANOVA; reproductive success by logistic regression; all other analyses by ANOVA or ANCOVA. To minimise effects of pseudo-replication, analyses of dropping intervals were performed on 1-hour block averages for each

Table 1. Average diet composition (% of dry weight) by habitat.

Habitat	<i>Festuca</i>	<i>Festuca</i> (low)	<i>Poa</i>	<i>Agrostis</i>	<i>Puccinellia</i>	Moss	<i>Phleum</i>	<i>Poa</i> (agricult)	n
Managed	40.5	13.2	43.7	1.0	0.9	0.7	0.0	0.0	11
Abandoned	64.2	16.3	10.9	7.3	0.7	0.6	0.0	0.0	87
Agricultural	1.7	0.0	0.0	0.0	0.0	0.8	86.6	11.0	23

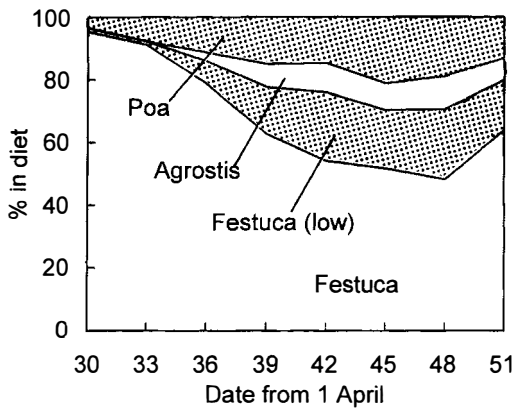


Fig. 1. Seasonal pattern in diet composition on managed and abandoned islands combined (total $n = 98$), averaged by 3-day periods. Not indicated are species that comprised on average less than 1% (e.g. *Puccinellia* and mosses).

individual pair. Data on unringed birds were treated as independent observations. This seems a valid assumption, as unringed birds were only followed when flocks were large (i.e. in agricultural and managed habitat) and the probability of replication was small.

Results

Diet composition

On the managed and abandoned islands, the main food species taken were *Festuca rubra* and *Poa* spp. (Table 1). The diet composition differed between the two habitats ($F_{5,83} = 7.49$, $P < 0.0005$), which was mainly due to a higher proportion of *Poa* in the diet of geese on managed islands ($F_{1,87} = 7.39$, $P < 0.01$). The diet composition in the two habitats combined changed with date (Fig. 1; $F_{5,83} = 10.47$, $P < 0.0005$). *Festuca*

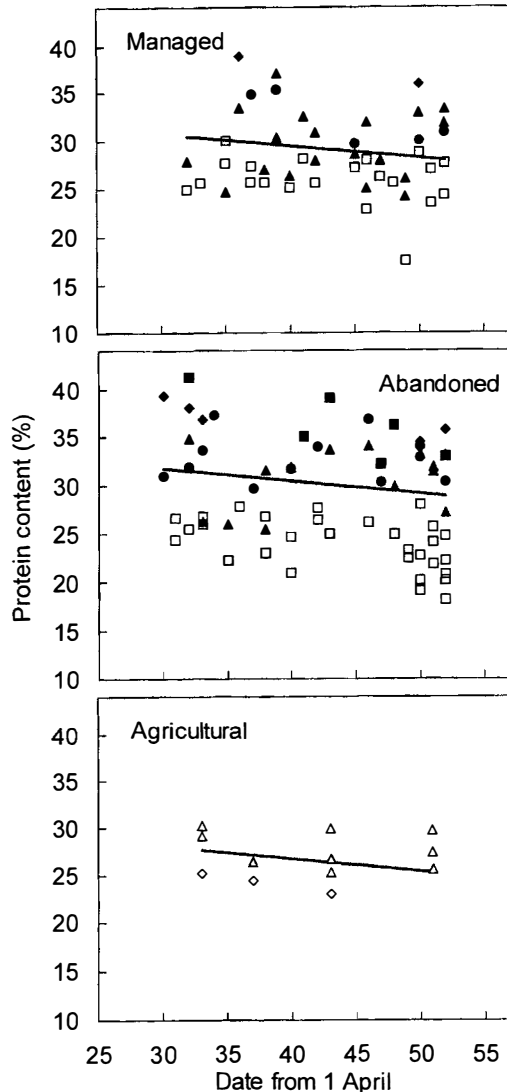


Fig. 2. Seasonal pattern in protein content (% of dry weight, ash-free) of main food plants in three habitats. *Poa* = filled triangle, *Festuca* = open square, *Festuca*-low = filled circle, *Puccinellia* = filled diamond, *Agrostis* = filled square, *Phleum* = open triangle, *Poa* agricultural = open diamond. Regression lines are based on model in Table 2A.

decreased in importance ($t_{87} = -6.94$, $P < 0.0005$), whereas the proportions of other species showed an increase. Geese feeding on agricultural fields mainly took *Phleum* and *Poa* spp. (Table 1). The proportion of *Poa* in the diet decreased slightly with date ($t_{21} = -2.41$, $P = 0.025$).

Chemical composition of food plants

Protein content of food species declined through time (Fig. 2). The rate of decrease was similar for all species (the date by species interaction term was not significant, $F_{6,119} = 1.84$, $P > 0.05$), whereas the intercepts differed (Table 2A). The species in order of decreasing protein content were: *Puccinellia*, *Agrostis* and *Festuca*-low, *Poa*, *Phleum* (agricultural area), *Festuca* and *Poa* (agricultural area). Within any species, protein content was independent of habitat (Table 2B).

Table 2. ANCOVA of protein content of plant species. Non-significant (N.S.) terms not included in the model are between brackets; given is the F -value when included in the final model. A. Comparing plants from all three habitats by date (covariate) and species; $n = 133$, r^2 model = 0.70. B. Comparing plants from managed and abandoned habitats only, by date (covariate), species and year; $n = 119$, r^2 model = 0.72.

A

Parameter	df	F-value	P
Date	1	9.38	0.003
Species	6	45.06	<0.0005
(Date \times Species)	6	1.84	N.S.
Model	7	41.2	<0.0005
Total	132		

B

Parameter	df	F-value	P
Date	1	11.42	0.001
Species	4	63.77	<0.0005
Year	3	3.48	<0.05
(Habitat)	1	0.79	N.S.
(Year \times Species)	11	1.16	N.S.
(Date \times Species)	4	2.44	N.S.
(Date \times Year)	3	1.74	N.S.
Model	8	35.26	<0.0005
Total	118		

There was a significant variation among years, which was similar for all species ($F_{11,99} = 1.16$, $P > 0.05$).

ADF content increased through time (Fig. 3). The rate of increase was similar for all species ($F_{6,61} = 1.42$, $P > 0.05$), whereas the intercepts differed (Table 3A). Species listed in order of increasing ADF content were: *Puccinellia*, *Agrostis*, *Phleum*, *Poa* (agricultural), *Poa*, *Festuca*-low

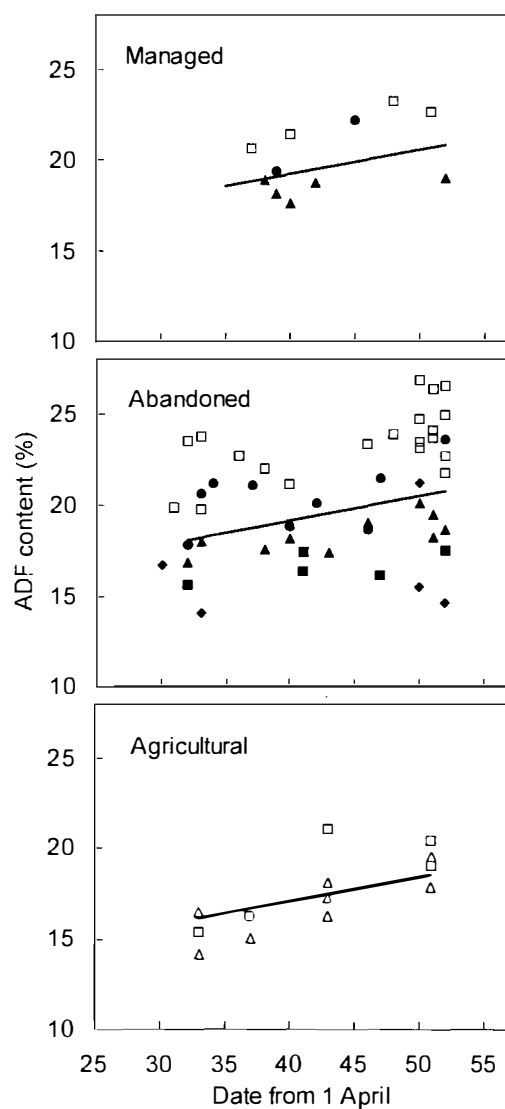


Fig. 3. Seasonal pattern in ADF content (% of dry weight, ash-free) of main food plants in three habitats. See Fig. 2 for explanation of symbols. Regression lines are based on model in Table 3A.

Table 3. ANCOVA of acid detergent fibre (ADF) content in food plants. A. Comparing plants from all three habitats by date (covariate) and species; $n = 75$, $r^2 = 0.79$. B. Comparing plants from managed and abandoned habitats only, by date (covariate), species and year; $n = 62$, $r^2 = 0.89$. Conventions as Table 2.

A			
Parameter	df	F-value	P
Date	1	29.49	<0.0005
Species	6	32.96	<0.0005
(Date \times Species)	6	1.42	N.S.
Model	7	36.38	<0.0005
Total	74		
B			
Parameter	df	F-value	P
Date	1	26.77	<0.0005
Species	4	68.50	<0.0005
Year	3	3.58	<0.05
(Habitat)	1	0.01	N.S.
(Year \times Species)	10	2.95	<0.01
(Date \times Species)	4	0.81	N.S.
(Date \times Year)	3	1.41	N.S.
Model	18	18.94	<0.0005
Total	61		

and *Festuca*. Similar species did not differ in ADF content between managed and abandoned habitat (Table 3B). Plants differed in ADF content among years, variation depending on the species ($F_{10,43} = 2.95$, $P < 0.01$): in *Festuca*, for example, the coefficient of variation of the annual means was 0.049, whereas in *Poa* this coefficient was as low as 0.027.

Dropping rate

Within the first hours of the day, dropping intervals decreased in length and tended to stabilise after 8 a.m. (Fig. 4). The mass of droppings showed an increase in the early morning. As a consequence, the egestion rate (dropping mass divided by interval) increased in the morning and stabilised after 7–8 a.m. We found no indication that the feeding effort changed with time (both % of time birds spent feeding, and peck rates

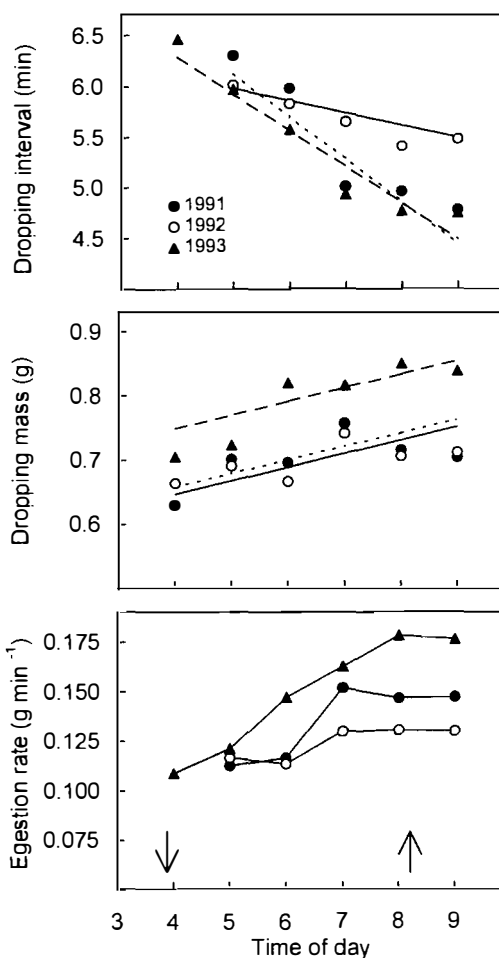


Fig. 4. Dropping interval (min) and mass (g dry weight) in relation to the time of day. Given are the means for 1-hour periods. Slopes of interval by time are different between years ($F_{2,298} = 7.53$, $P < 0.001$): -0.61 , -0.12 , -0.36 . Slopes of dropping mass by time are similar across years ($F_{2,813} = 2.95$, $P > 0.05$). Production rate of droppings (egestion rate, g min^{-1}) stabilises after 8 a.m. Average timing of arrival on and departure from the main study site is indicated by arrows.

remained constant in the morning; JP, unpubl.). We conclude therefore that the increase in egestion rate was a consequence of filling of the intestinal tract and that the egestion rate reflected food ingestion rate only after 8 a.m. To derive food intake from dropping production, we did the following: (1) based on the relationship between intervals and time of day, we adjusted dropping intervals to 8 a.m.; (2) dropping weights were based on samples without information on the exact time of production, and a simple time-

Table 4. ANCOVA of dropping intervals, corrected for time of the day (Fig. 4), by year, habitat and date (covariate); $n = 595$, $r^2 = 0.12$. Conventions as Table 2.

Parameter	df	F-value	P
Date	1	20.49	<0.0005
Year	5	10.69	<0.0005
(Habitat)	2	2.03	N.S.
(Date \times Year)	5	0.40	N.S.
Model	6	13.44	<0.0005
Total	594		

adjustment was therefore not possible. To minimise bias towards light droppings, and hence underestimate ingestion rates, we did not process samples that originated from areas that had been grazed exclusively in early morning.

Dropping interval

Dropping intervals increased by date (Table 4, Fig. 5). Habitat did not affect dropping intervals, instead there was variation among years. The interaction term of date and year was not significant ($F_{5,583} = 0.40$, $P > 0.05$), and we conclude therefore that the daily increase in intervals was similar over years.

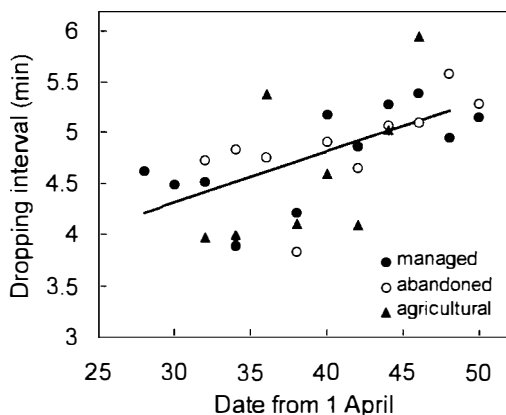


Fig. 5. Dropping interval by 2-day periods for each of the habitats. Intervals adjusted to 8 a.m. (see Fig. 4) and corrected for annual differences. Total numbers of observations in the managed, abandoned and agricultural habitat are 233, 307 and 55, respectively. The regression line is $y = 0.050x + 2.807$, based on model in Table 4.

Table 5. ANCOVA of dropping mass by year, habitat and date (covariate); $n = 828$, $r^2 = 0.35$. Conventions as Table 2.

Parameter	df	F-value	P
Date	1	43.65	<0.0005
Year	4	8.46	<0.0005
Habitat	2	15.04	<0.0005
Date \times Year	4	11.73	<0.0005
(Year \times Habitat)	1	0.11	N.S.
(Date \times Habitat)	2	0.65	N.S.
Model	11	40.57	<0.0005
Total	827		

Dropping mass

Dropping mass increased by date (Table 5, Fig. 6), and varied by year and habitat. Droppings were heaviest on agricultural fields and lightest on abandoned islands. The interaction between date and year of observation was significant ($F_{4,816} = 11.73$, $P < 0.0005$), which means that the date effect differed between years.

Digestibility and ingestion rate of organic matter

Digestibility of the food showed a quadratic response with date; highest values occurred by mid-May (Fig. 7). The date effect was similar across years (interaction term: $F_{3,80} = 1.79$, $P > 0.05$) and among habitats ($F_{2,81} = 0.76$, $P > 0.05$). Digestibilities differed among years within each of the habitats (Table 6A). Averaged over years, digestibilities were highest on agricultural fields, followed by abandoned and managed islands.

Ingestion rates of organic matter and digestion rates showed a quadratic response with date (Fig. 7). The trend was similar among habitats ($F_{2,81} = 0.39$, and $F_{2,84} = 0.35$, respectively, $P > 0.05$) and across years (interaction term for organic matter: $F_{3,80} = 0.27$, $P > 0.05$). Ingestion rates of organic matter differed among years (Table 6B), whereas the year-effect in digestion rates was not significant (Table 6C). Differences in ingestion rates were cancelled out because annual averages of ingestion rate and digestibility were inversely related. Ingestion and digestion rates were highest

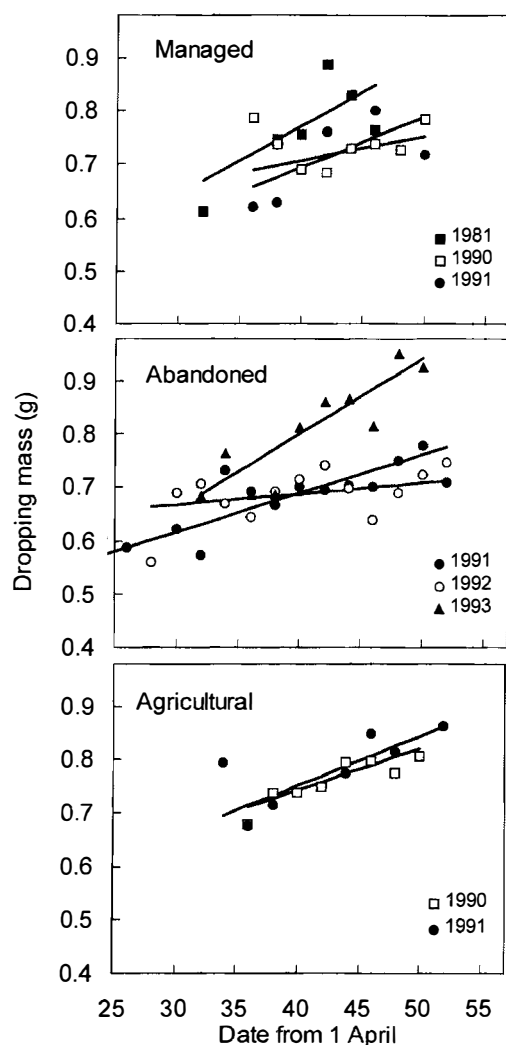


Fig. 6. Dropping mass (g dry weight) by 2-day periods for each of the habitats. Total numbers of samples in the managed abandoned and agricultural habitat are 111, 633 and 84, respectively. Regression lines are based on model in Table 5.

in the agricultural habitat, intermediate on managed islands and lowest on abandoned islands.

Assimilation efficiency and ingestion rate of nitrogen

The assimilation efficiency of nitrogen, and the ingestion and assimilation rate of nitrogen showed a quadratic response with date (Fig. 8). The

assimilation efficiency of nitrogen differed among years, and differences between habitats were almost significant (Table 7A). Pooling data revealed higher efficiencies in managed and abandoned habitats compared to agricultural habitat ($F_{1,84} = 4.25$, $P < 0.05$). The ingestion rate of nitrogen differed among years and habitats (Table 7B). The assimilation rate of nitrogen differed among habitats (Table 7C), being highest on managed islands. There were no significant year-effects. None of the interaction terms between a factor and date was significant.

Rate of excretion of nitrogen

The rate of excretion of nitrogen was closely related to the ingestion rate of nitrogen (Fig. 9). The slopes of the relationship were similar for habitats ($F_{2,82} = 1.33$, $P > 0.05$); whereas the intercepts were different at 0.0029, 0.0027 and 0.0038 g min^{-1} for managed, abandoned and agricultural habitats, respectively ($F_{2,84} = 7.64$, $P < 0.001$). Likewise there was a year-effect. In order to have a conservative estimate for nitrogen excretion (i.e. not too high in the agricultural habitat), the average value of 0.00315 g min^{-1} was used in further calculations.

Accumulation of body reserves

The accumulation of protein reserves, calculated from nitrogen retention, was highest on managed islands, intermediate on abandoned islands and lowest on agricultural fields (Fig. 10). Estimated amounts for May summed up to 125, 104 and 18 g, respectively. The accumulation of fat was highest on agricultural fields (407 g), intermediate on managed islands (155 g), and lowest on abandoned islands (147 g).

Similarly, the size of fat reserves may be derived from AP scores. Fat levels at arrival (observations before 5 May averaged by individual) were lowest for geese in the agricultural habitat (Fig. 11). In contrast, birds in the agricultural area had achieved highest AP's at departure (observations after 14 May averaged). There was no significant difference in AP between birds on managed or abandoned islands. Thus, changes in AP in each of the habitats corresponded

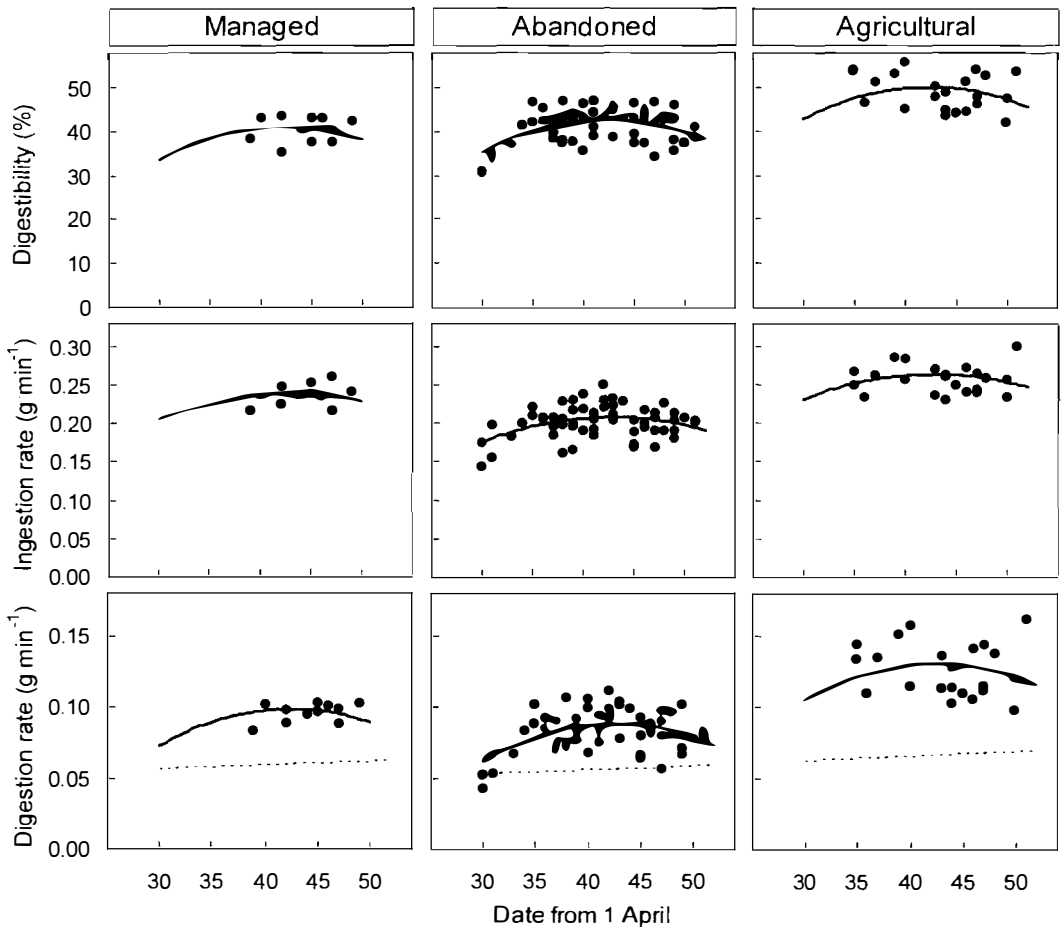


Fig. 7. Digestibility of organic matter, ingestion rate of food (ash-free), and digestion rate (ingestion rate of metabolisable food) by date for each of the habitats. Ingestion rates and digestibilities have been adjusted for annual differences. The dashed lines in the lower panels indicate the amounts of food that have to be metabolised to maintain body mass. Regression lines are based on models in Table 6.

well with the trends in calculated amounts of fat deposited.

Reproductive success

In this analysis the aim was to determine whether reproductive success varied as a function of year, staging habitat and body condition. It is well known that reproductive success in arctic geese varies greatly from year to year (Davies & Cooke 1983; Ebbinge 1989), and this was confirmed in this study (logistic regression, $\chi^2 = 33.92$, $df = 6$, $P < 0.0005$; Fig. 12). Controlling for year, pairs

using different habitats did not differ in subsequent reproductive success ($\chi^2 = 1.36$, $df = 2$, $P > 0.05$). Reproductive success was not related to annual mean values of AP at departure, neither for all birds ($r = -0.27$, $n = 6$, $P > 0.05$) nor for each habitat separately. This means that overall, annual variation in reproductive success was not affected by the body condition that geese achieved during spring. The observations during a plague of voles *Arvicola terrestris* on the abandoned islands in 1988–1990 when much of the vegetation was destroyed indicate, however, that extremely poor food conditions in spring may affect subsequent reproductive success.

Within any particular year, the probability of

Table 6. ANCOVA of (A) Digestibility of organic matter, (B) Ingestion rate of organic matter, (C) Digestion rate. Habitat and Year are factors, Date and Date² are covariates; $n = 91$, $r^2 = 0.53, 0.71$ and 0.67 . Conventions as Table 2.

A			
	<i>df</i>	<i>F</i> -value	<i>P</i>
Date	1	14.69	<0.0005
Date ²	1	14.17	<0.0005
Habitat	2	12.37	<0.0005
Year	3	4.31	<0.01
(Date + Date ² × Habitat)	2	0.76	N.S.
(Date + Date ² × Year)	3	1.79	N.S.
Model	7	13.41	<0.0005
Total	90		
B			
	<i>df</i>	<i>F</i> -value	<i>P</i>
Date	1	9.58	0.003
Date ²	1	9.01	0.004
Habitat	2	39.69	<0.0005
Year	3	7.64	<0.0005
(Date + Date ² × Habitat)	2	0.39	N.S.
(Date + Date ² × Year)	3	0.27	N.S.
Model	7	28.74	<0.0005
Total	90		
C			
	<i>df</i>	<i>F</i> -value	<i>P</i>
Date	1	13.85	<0.0005
Date ²	1	13.17	<0.0005
Habitat	2	72.85	<0.0005
(Year)	3	0.26	N.S.
(Date + Date ² × Habitat)	2	0.35	N.S.
Model	4	42.74	<0.0005
Total	90		

raising goslings was closely related to AP at departure ($\chi^2 = 5.15$, $df = 1$, $P < 0.025$). This relationship was further explored by examining the slopes of the curves. We can imagine that an effect of body reserves on reproductive success depends on environmental conditions during breeding, which would mean that the relationship differed between years with low or high reproductive success. This is not the case, however, as the slopes of reproductive success on AP are

similar in years with reproductive success above or below average ($\chi^2 = 0.54$, $df = 1$, $P > 0.05$). Instead, the interaction term between AP and habitat was significant ($\chi^2 = 7.39$, $df = 2$, $P < 0.025$), which means that the slopes differed between habitats. Testing each habitat separately revealed a positive relationship between reproductive success and AP for geese using managed and abandoned habitats, but not for geese in the agricultural area (Fig. 13). In particular, geese in the agricultural habitat achieving a high AP score suffered a depressed probability of successful breeding compared to birds in the other habitats.

Discussion

Agricultural habitats usually provide geese with a more profitable food source in comparison to natural habitats (Hobaugh 1985; Madsen 1985; Alisauskas et al. 1988; Bédard & Gauthier 1989; Alisauskas & Ankney 1992; Krapu et al. 1995; Robertson & Slack 1995). Our data support this general view as geese in this study accumulated the largest amounts of energy reserves when staging in the agricultural habitat. However, we found no consistent differences in reproductive success between geese that had used agricultural or semi-natural habitats. This is surprising given the link between body condition in spring and subsequent breeding performance as found in brent geese *Branta b. bernicla* (Ebbinge & Spaans 1995). This paradox calls for further consideration.

Accumulation of body reserves

Among habitats, geese accumulated energy reserves at different rates because of two main factors. Both ingestion rate and digestibility of the food were highest in the agricultural habitat, lowest on abandoned islands and intermediate on managed islands. We think these results are a direct consequence of the management applied in each of the habitats. Pastures in the agricultural areas were grazed by cattle in summer, cut for silage and heavily fertilised. Thus, they were managed to provide a homogeneous supply of food with a high density of grasses and little dead

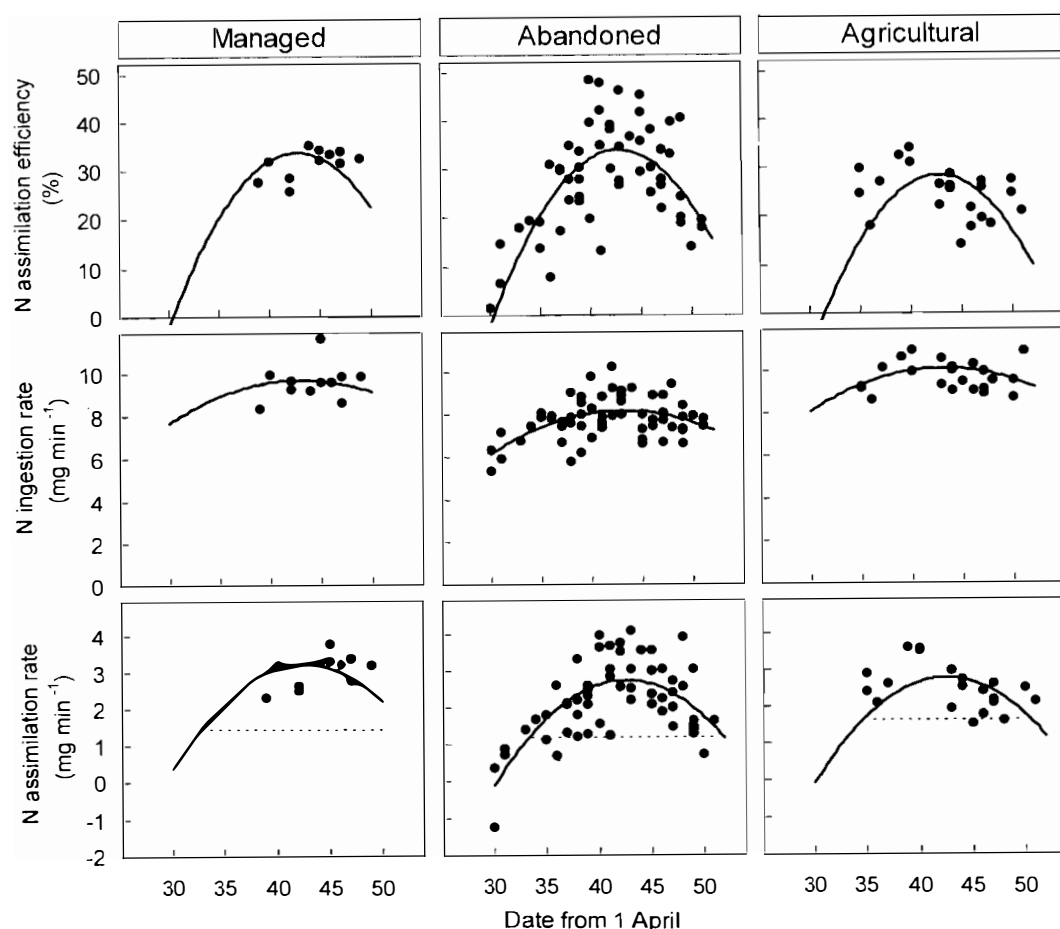


Fig. 8. The apparent assimilation efficiency of nitrogen, and ingestion rate and assimilation rate of nitrogen (ingestion rate of assimilated nitrogen) by date for each of the habitats. Ingestion rates and assimilation efficiencies have been adjusted for annual differences. The dashed lines in the lower panels indicate the amounts of nitrogen that have to be assimilated to achieve nitrogen balance. Regression lines are based on models in Table 7.

material. Combined with the low fibre content of the crops, this provided geese with a high-quality food supply. The islands within the traditional range of geese that were still inhabited by people were much less intensively used; they were grazed by sheep, and once a year grass was cut on flat parts of the islands ('Hay meadows'). Likewise, *Puccinellia* and *Agrostis*, two species occurring in natural vegetation zones, were highly digestible, but because of a limited distribution these species were less important in the diet. *Festuca* was the staple food on the traditional islands but this plant was less digested than other grasses. On abandoned islands Hay meadows were absent, and geese were totally relying on natural vegetation.

Geese on managed and abandoned islands spent more time foraging compared to birds on agricultural islands (84% vs 70% of the daylight hours: Black et al. 1991), but this was apparently not sufficient to compensate for the lower ingestion rate and digestibility of the food.

The observation of a lower apparent assimilation efficiency of nitrogen by geese in the agricultural area is a surprising result. Perhaps the lower assimilation efficiency was caused by a depressed digestibility of nitrogen compounds in the food, and a concomitant lower assimilation from the gut into the blood. To test this possibility, we approximated the nitrogen content of the faeces by analysing droppings for total nitrogen after

Table 7. ANCOVA of (A) Assimilation efficiency of nitrogen, (B) Ingestion rate of nitrogen, (C) Assimilation rate of nitrogen. Habitat and Year are factors, Date and Date² are covariates; $n = 91$, $r^2 = 0.46, 0.69$ and 0.47 . Conventions as Table 2.

A			
	df	F-value	P
Date	1	59.76	<0.0005
Date ²	1	56.38	<0.0005
Habitat	2	2.98	<0.06
Year	3	4.19	<0.01
(Date + Date ² × Year)	3	1.68	N.S.
(Date + Date ² × Habitat)	2	1.82	N.S.
Model	7	14.55	<0.0005
Total	90		
B			
	df	F-value	P
Date	1	16.30	<0.0005
Date ²	1	15.23	<0.0005
Habitat	2	19.41	<0.0005
Year	3	10.99	<0.0005
(Date + Date ² × Year)	3	0.21	N.S.
(Date + Date ² × Habitat)	2	0.30	N.S.
Model	7	26.33	<0.0005
Total	90		
C			
	df	F-value	P
Date	1	54.72	<0.0005
Date ²	1	52.18	<0.0005
Habitat	2	2.95	<0.05
(Year)	3	0.93	N.S.
(Date + Date ² × Habitat)	2	2.12	N.S.
Model	4	18.83	<0.0005
Total	90		

careful removal of the white urinary products on the distal end of the droppings (Lane 1994) and subsequently estimating the true assimilation efficiency (*sensu* Karasov 1990). These data showed no difference in true assimilation efficiency of nitrogen between the two habitats (agricultural $\bar{x} = 69.8$; abandoned $\bar{x} = 68.3$; $F_{1,6} = 0.34$, $P > 0.05$). We therefore conclude that nitrogen was assimilated at similar efficiencies in all habitats, but that geese on the agricultural fields

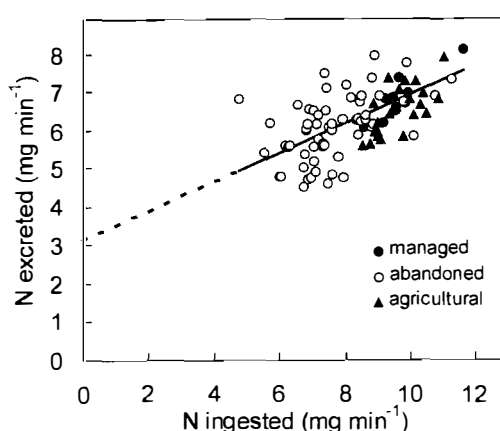


Fig. 9. Excretion rate of nitrogen in relation to ingestion rate of nitrogen ($y = 0.38x + 3.15$, $n = 91$, $F_{1,84} = 23.32$, $P < 0.0005$). Excretion rates have been adjusted for variation among years ($F_{3,84} = 6.53$, $P < 0.001$) and habitats ($F_{2,84} = 7.64$, $P < 0.001$). Slopes are similar for each of the habitats ($F_{2,82} = 1.33$, $P > 0.05$).

excreted urinary products at a higher rate. Therefore, it seems that geese on agricultural fields either chose not to use the assimilated nitrogen, or they were not able to do so.

Nitrogen that is retained is used for deposition of protein tissue. The energy content of protein tissue (5.8 kJ g^{-1}) is much lower than that of fat (39.3 kJ g^{-1}). This is caused by the lower physiological energy content of proteins (18 kJ g^{-1}) and the considerable amount of water that is associated with protein (68%, Raveling 1979; Campbell & Leatherland 1980; Korte 1988). If it were for storage of energy alone, fat should be deposited as the only energy store, and any protein ingested in excess to the amount needed to compensate for catabolic losses should be channelled into the carbohydrate metabolism after deamination (Blaxter 1989). This means that geese on the traditional islands obviously retained the considerable amount of nitrogen for other reasons than just preparing the most compact energy store. We infer therefore that geese in the agricultural habitat were not able to produce protein tissue from the assimilated nitrogen at the same rate as in the other habitats. Several studies have pointed to the unbalanced composition of amino acids in plants in comparison with muscle tissue (protein), and cystine and methionine in particular, are in short supply in vegetable matter (van Soest 1980; Sedinger 1984; Thomas & Prevet 1980). We suggest that the grasses in our agricultural study

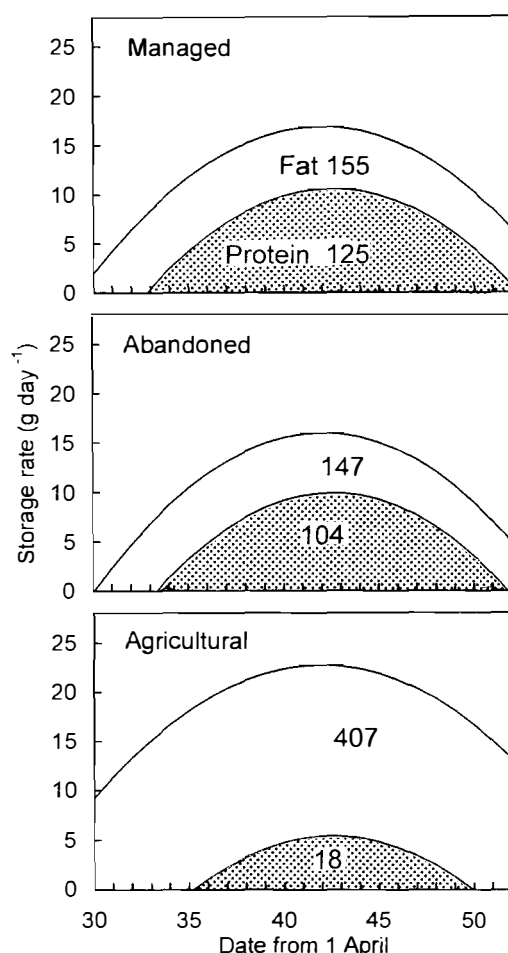


Fig. 10. Rate of storage of fat and protein (g d^{-1}) for birds staging in one of the three habitats. The accumulated sums for each component are separately indicated.

area (newly sown *Phleum* and *Poa*) were more unbalanced in amino acid composition than grasses in the (semi-) natural habitats, thus causing the observed differences in protein deposition.

This poses the question whether the differences in protein deposition rates are typical for the habitats involved. There is some evidence for this. First, low protein deposition rates were observed in other goose species feeding on agricultural crops. In some cases this was attributed to low protein contents of the food (grains, Madsen 1985; Alisauskas & Ankney 1992), in other cases it was attributed to imbalances in the amino acid composition of the crops eaten (Alisauskas & Ankney 1992; McLandress & Raveling 1981; Alisauskas et

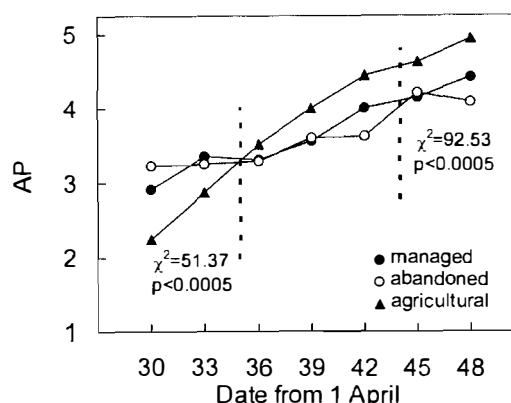


Fig. 11. Abdominal profile (males and females averaged) by 3-day periods for each habitat. Sample sizes in the managed, abandoned and agricultural habitat are 4586, 2198 and 8700, including replicates. Differences between habitats in AP before 5 May, and after 14 May were tested by averaging values per individual. Differences were consistent in the four years when data were collected in each of the habitats.

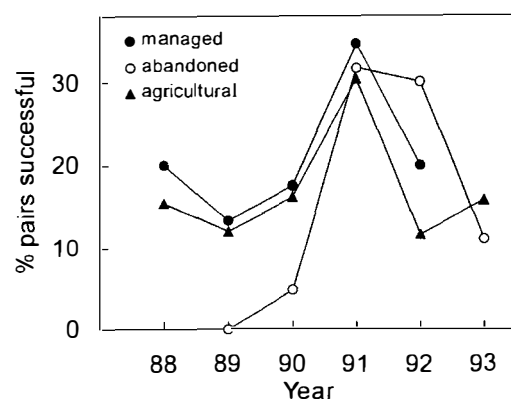


Fig. 12. Probability of successfully raising at least one gosling through autumn by year and spring habitat. The analysis is based on ringed females; age between 3 and 17 years to reduce age-effects (see Black & Owen 1995). Number of observations per data point varied between 10 and 161; totals per managed, abandoned and agricultural habitat were 203, 124 and 811. From 1988 through 1990 a vole plague occurred on the abandoned islands.

al. 1988). Secondly, at the onset of protein deposition in early spring many goose species show a shift in habitat. Usually this is from farmland to (semi-) natural habitats (Wypkema & Ankney 1979; McLandress & Raveling 1981; Ebbinge et al. 1982; Boudewijn 1984; Prins & Ydenberg 1985; Vickery et al. 1995). Several explanations have been proposed to explain this phenomenon,

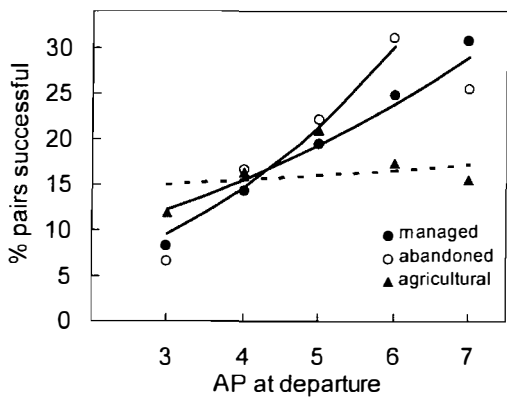


Fig. 13. Probability of successful reproduction in relation to AP of females prior to migration. Slopes of the fitted logistic curves for managed, abandoned and agricultural habitats are 0.236 ($\chi^2 = 3.63$, $P = 0.05$), 0.465 ($\chi^2 = 3.74$, $P = 0.05$), 0.039 ($\chi^2 = 0.17$, $P > 0.05$), respectively. Sample sizes for each habitat are: 24, 93, 113, 42 and 13, 15, 24, 27, 17 and 4, 40, 55, 109, 133 and 116.

but we think the most satisfactory factor explaining these shifts towards natural habitat is the need for specific nutrients (i.e. amino acids) to deposit protein stores. McKay et al. (1994) arrived at a

similar conclusion when interpreting a habitat shift by brent geese in winter.

The total body mass gain appeared to be remarkably similar in the three habitats (Table 8), though it should be noted that birds on the traditional islands kept up with agricultural birds by storing more water associated with protein. Table 8 lists the literature references dealing with body mass gain rates of geese during spring migration. All estimates we found in literature are based on samples of birds collected at successive times in the season, which means that growth rates may have been slightly underestimated (Zwarts et al. 1990). Rates of body mass gain were negatively correlated with the (log-transformed) body mass for each species ($y = 1.36 - 1.51x$, $n = 7$, $P < 0.05$). The body mass gain rate of the barnacle geese in this study (average $1.24 \text{ g d}^{-1} 100 \text{ g}^{-1}$ body mass) is within the range predicted on the basis of the regression for the other species (average and 95% CI: 0.98 ± 0.48).

The ratio of deposition of fat and protein is highly variable among goose species and within seasons (Table 8). Our data are within the range found for other species. We observed a rather constant ratio of fat to protein deposition through-

Table 8. Rate of body mass increase in spring staging geese. Data are expressed as daily increase of g (fresh) weight per day, and as a proportion of the winter body mass (from Owen 1980). Composition of body reserves is indicated by the ratio of fat/protein.

Species	Month	Habitat	Gain rate, g d^{-1}	Gain rate, $\text{g d}^{-1} 100 \text{ g}^{-1}$ body mass	Fat/protein (range)	Source
Snow goose <i>A. c. caerulescens</i>	5	marshes	14	0.7	0	Wypkema & Ankney 1979
Greater snow goose <i>A. c. atlanticus</i>	4–5	marshes	11.5	0.4	64	Gauthier et al. 1992
White-fronted goose <i>A. albifrons frontalis</i>	2–3	agricultural	20.2	0.8	11.8	Krapu et al. 1995
Giant Canada goose <i>B. canadensis maxima</i>	3–4	agricultural	28.8	0.8	4.5 (0.2–8.9)	McLandress & Raveling 1981
Cackling goose <i>B. c. minima</i>	4	marshes	17.5	1.3	9.6	McWilliams 1993
Barnacle goose <i>B. leucopsis</i>	4–5	salt marshes	17	0.95		Ebbinge et al. 1991
Barnacle goose	5	managed	24.8	1.4	1.2	this study
		abandoned	21.5	1.2	1.4	this study
		agricultural	21.1	1.2	22.6	this study
Black brant <i>B. b. nigricans</i>	4–5	(captive)			2.0 (0.9–4.9)	Sedinger et al. 1992
Brent goose <i>B. b. bernicla</i>	5	salt marshes	16.5	1.3		Ebbinge 1989

out the staging period (Fig. 10). In contrast, Sedinger et al. (1992) showed in captive black brant *Branta bernicla nigricans* a decrease in the ratio through time, and in May this species deposited more protein than fat. Table 8 suggests there is a tendency that smaller goose species deposit more protein relative to fat. This corresponds well with the compilation of Zwarts et al. (1990) who showed that waders deposit even more protein than geese (40% of body reserves in waders is composed of protein, or a ratio of 1.5).

Body condition and reproductive success

The relationship between body condition and reproductive success differed largely depending on whether between-years or within-year effects are considered. Reproductive success was not correlated with annual averages of fat scores at departure. This is not surprising as weather and snow conditions at the breeding grounds are important causes of variation in breeding success (Prop & de Vries 1993). In contrast, Ebbsinge (1989) found in brent geese a positive relationship between reproductive success and body condition in spring when years with total reproductive failure were excluded from the analysis (e.g. years with adverse migration conditions and high predation pressure by arctic foxes *Alopex lagopus*). However, within any year we found a strong correlation between fat scores at departure and subsequent reproductive success. This means that given particular conditions during breeding, birds with largest fat reserves were at an advantage. Madsen (1994) found a similar relationship between reproductive success and fat reserves in pink-footed geese staging in Vesterålen, Norway, like Ebbsinge & Spaans (1995) did in spring staging brent geese.

Our data show a remarkable discrepancy between habitats in the relationship between reproductive success and fat levels. Trends were similar in managed and abandoned habitats, showing a strong positive relationship between the probability of successful reproduction and AP. However, in the agricultural area the effect of body condition appeared to be almost absent; in particular birds with largest reserves had a much lower reproductive success compared to individuals from other habitats (Fig. 13). The agricultural habitat was recently colonised, and Black et al. (1991) have

suggested that geese in this area were initially of lower quality. However, even if this were the case during the years of this study, we could expect a positive relationship between body condition and reproductive success. Instead, one could argue that fat levels achieved in spring and the probability of successful reproduction are interrelated as both parameters may reflect the individuals' competitive abilities. The lack of a positive relationship in birds using the agricultural habitat could be the result of a relatively rich food supply on the fields enabling even low competitive birds to achieve high fat levels. As an alternative explanation for the absence of a positive relationship between reproductive success and fat levels in birds using the agricultural habitat, we suggest there might be a nutrient limitation, which results in birds failing to benefit from large fat stores. A link with the overall low protein stores of birds in the agricultural habitat is likely, and two mechanisms are possible. We suggest that geese from the agricultural area are either falling short in mechanical power (i.e. muscle development) and unable to carry their own fat reserves (a deficit of structural protein), or they have insufficient non-structural protein reserves for successful reproduction.

In early spring, barnacle geese exhibit a similar distribution in Scotland, where about half the population concentrates on agricultural foods and the other half occurs on traditional salt marshes (Owen et al. 1987). If excessive fat and little protein produced sub-optimal muscle development, and if preference for agricultural food persisted from the staging grounds in Scotland to Helgeland, we might expect that geese arriving at the agricultural area in Norway would be in worse body condition. Indeed, the birds arriving at the spring agricultural sites had the lowest APs (Fig. 11). This may indicate that low levels of protein obtained on agricultural land in Scotland resulted in thinner profiles on arrival in Helgeland. Such a relationship might also occur on the final migration step from Norway to the breeding grounds. Observations of birds arriving in Spitsbergen are lacking, but data on body condition have been collected three weeks later when birds moved to the colonies (I. Tombre, unpubl.). Birds from agricultural habitat arrived 3 days earlier at the nest site compared to birds from semi-natural habitat (Mann-Whitney $U = 3.21$, $n_1 = 54$, $n_2 = 126$, $P < 0.005$). At the same time, late birds arrived in the colony in a better body condition (Tombre et al. 1996). This indicates that agricul-

tural birds had lost much of their excess body reserves before egg-laying had begun. More work is required to understand the interrelationships between spring habitat use, composition of body stores, migration pattern and reproduction performance.

Population and management implications

On the basis of the reproductive success of geese using different habitats, we conclude that the agricultural habitat is not the most profitable area. Rather, it functions as a spill-over area, being used by the rapidly growing population after the carrying capacity of the traditional range had been reached (Prop et al. 1998). This is similar to observations on brent geese in spring by Ebbsinge (1992). Ebbsinge suggested that brent numbers on salt marshes did not exceed a certain density; with a growing population surplus birds moved to agricultural areas.

Our data indicate that the low reproductive success of birds using the agricultural habitat relative to the amount of fat stored may be due to a nutrient limitation. It is thus extremely important that geese preparing for migration have access to a diverse set of food resources. Geese on the agricultural islands in Norway do to some extent have a varied diet, by feeding on nearby salt marshes (Black et al. 1991); however, the marshes are only narrow strips bordering the shores and are far from sufficient to accommodate all the geese. In contrast, the low-intensity management on the traditional islands has proven to be beneficial to geese. Geese have access to natural vegetation communities, dominated by *Festuca* or *Puccinellia*, while the meadows developed under an extensive management regime allow geese to gain rapidly fat and protein reserves. When people abandon the islands the numbers of geese decline drastically (Prop et al. 1998). Moreover, the body reserves deposited by geese appear to decline by 5 and 17% (fat and protein, respectively). This illustrates the importance to geese of maintaining the traditional 'crofter's' management.

Refuge establishment is often advocated for reducing conflicts between geese and agricultural interests (Owen 1990; Owen & Pienkowski 1991). On the wintering grounds such schemes have been successful in attracting and holding geese from areas where they are not welcome (Owen et al.

1987). Although these refuges may produce birds with large AP's, they may not produce geese with the optimal requirements for successful breeding. Further work on the consequences of the goose diet may therefore be warranted. To understand the significance of specific nutrients to pre-migratory geese, two main problems should be addressed in future work: the effects of amino acid balance in the diet of geese on the birds' physiology; and the optimal ratio in deposition of fat and protein reserves.

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Modelling the dynamics of winter barnacle goose flocks: A progress report

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Models of foraging behaviour in animals can help us understand the distribution of individuals across the available resources and hence to predict the likely effects of changes in conditions on population size. Models of this kind are well developed for cases where individuals interfere with each other's ability to forage effectively by reducing intake rate at high density, or alternatively where there is no direct interaction between conspecifics. However, although the movement of geese within and between flocks is affected by dominance interactions, they do not show classical interference. These models therefore cannot adequately describe the foraging dynamics of flocking geese. This paper describes the development of a novel approach to this problem, based on a trade-off between the vigilance benefits and the depletion costs of feeding in larger flocks. The need for this development is discussed in relation to the fundamental characteristics of goose flocks which distinguish them from other foraging systems. The approach is placed in the context of a broader project modelling the year-round dynamics of the Svalbard barnacle goose population from the perspective of individual behaviour.

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Introduction

The principles of population ecology can help us understand how changes in management practices can affect the size and growth patterns of wild populations. For example, models incorporating known effects of environmental factors on key demographic variables can be used to explore the implications of environmental changes for the population. Similarly, observed density dependent responses of demographic parameters can be used to explore population equilibria. However, the utility of this approach is limited because data are usually only available for a limited environmental or population range, and it cannot be assumed that the relationships thus obtained will apply outside the narrow range observed (Goss-Custard 1993).

An alternative approach seeks to work from behavioural decisions at the level of the individual, through the resultant patterns of dispersion, to a prediction of individual-level feeding performance. If we assume that individuals not reaching

a certain level of performance will fail to breed or, more severely will not survive, the implications of individual-level performance for population-level rates of productivity and mortality can be predicted. A link can thus be made between behaviour and population dynamics (Goss-Custard 1985; Sutherland & Dolman 1994). Because predictions of this sort stem from evolutionary factors which determine individual behaviour, it can be assumed that such predictions apply also for conditions outside the environmental or population range hitherto observed.

The overall aim of this project is to provide a model framework by which variation in the foraging performance of individual barnacle geese *Branta leucopsis* from the Svalbard population can be predicted throughout the annual cycle. Such a framework should enable us to predict the proportions of the population which survive and reproduce given current or altered levels of habitat availability. Our present ability to predict the effects of management is poor (see Pettifor et al. 1998, this volume) and the need to improve the

situation is becoming increasingly urgent (Black 1998). This modelling approach thus provides us with a potentially important and much needed management tool. The approach is made possible by the large amount of information existing on this population. Svalbard barnacle geese have been studied intensively over a long period in their wintering grounds (e.g. Boyd 1968; Owen & Kerbes 1971; Black & Owen 1984; 1989a, b; Owen *et al.* 1987; 1992), spring staging grounds (e.g. Gullestad *et al.* 1984; Black *et al.* 1991; Tombre *et al.* 1996) and breeding grounds (e.g. Larsen & Norderhaug 1963; Prop *et al.* 1984; Prestrud *et al.* 1989; Prop & de Vries 1993; Choudhury *et al.* 1993; Tombre & Erikstad 1996; Dalhaug *et al.* 1996; Loonen *et al.* 1997). A wealth of information has been provided on the behaviour and ecology of the geese at all stages of the annual cycle, at both the individual level and the population level.

The complete model will simulate patterns of resource acquisition, fecundity and survival throughout the annual cycle (see also Lang *et al.* 1998, this volume). A critical component of this year-round model is the outcome of competition for resources on the wintering grounds, where the geese form large flocks. At this time, the foraging performance of individuals depends on the nature of their interactions with other geese (Black & Owen 1988; Black & Owen 1989a). This paper describes an approach to the modelling of flock dynamics in barnacle geese.

Foraging models

Through a body of theoretical work based on optimisation, foraging theory has traditionally attempted to understand the distribution of individuals among different feeding areas (Milinski & Parker 1991). Individuals are assumed to feed in the place where they can maximise, most commonly, their rate of food intake, their chances of avoiding predation, or a combination of these (e.g. McNamara & Houston 1990). The theoretical basis for much work on the distribution of consumers is the ideal free distribution model introduced by Fretwell & Lucas (1970). In this model, individuals choose to feed where they can maximise their fitness, which is generally measured in terms of food intake rate. When foraging

individuals seek to maximise their intake rate, a trade-off between food availability and competitor density is necessary. Where food availability is higher, a higher intake rate can be achieved, but this may be countered by interference between individuals and lead to reduced intake at high competitor density (Sutherland 1983). Related models allow for cases where there is territoriality (despotic distributions—Ens *et al.* 1995), or where there is no interference (depletion models—Sutherland & Allport 1994). In the case of despotic distributions, some individuals are able to monopolise resources through the physical exclusion of others. In the case of depletion models, there is no direct cost to feeding at high competitor density, and all individuals are therefore predicted to aggregate in the best available area, spreading out over a wider area as depletion progresses and patch profitabilities are equalised (Sutherland & Anderson 1993).

While these models of consumer distribution have provided a useful framework for the interpretation of many patterns of aggregation in animals, none is readily applicable in the case of animals which form dense aggregations, such as flocking geese. As there is clearly no territoriality in such aggregations, the despotic model is not applicable. Similarly, as there is no evidence for a negative effect of competitor density on intake rate, the standard ideal free model cannot apply. Finally, although depletion is clearly an important process in goose flocks, the standard depletion model does not fit the facts. In a depletion model, individuals are assumed to disperse more widely as depletion progresses, and there is assumed to be no variation in foraging performance related to dominance. The behaviour of flocking geese contradicts both these assumptions (Teunissen *et al.* 1985; Prop & Loonen 1989; Black *et al.* 1992). A new approach which accounts for these discrepancies is thus required to model the foraging distribution of flocking geese.

A foraging model for flocks

The prime reason for the formation of dense aggregations such as flocks is the minimisation of predation risk (Hamilton 1971; Pulliam 1973). Individuals alone or in small groups have a high perceived risk of predation, and levels of vigilance

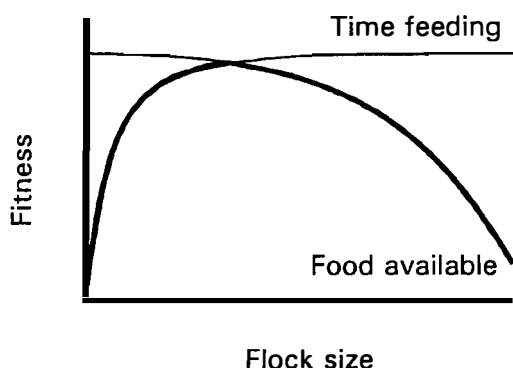


Fig. 1. Hypothetical relationships for time feeding and food availability in relation to flock size. Increasing time feeding reflects decreasing time vigilant, while decreasing food availability reflects increasing depletion. The bold line indicates the fitness function for flock size.

are thus high. This reduces the time available for feeding. By contrast, vigilance costs can be shared in large aggregations, resulting in individuals spending more time feeding (Lazarus 1972). As a result, negative relationships between vigilance and group size have been recorded for a wide range of species (reviewed by Lima & Dill 1990), including geese (Lazarus 1978; Inglis & Lazarus 1981). Much theoretical and empirical work has focused on the reasons for the emergence of group size-vigilance relationships (see reviews by Pulliam & Caraco 1984; Bednekoff & Lima 1998); however, the consequences of this behaviour for the foraging performance of individuals has not been developed theoretically. The work presented here aims to provide such a development, using a game-theoretic approach to the distribution of individuals. This use of game theory matches the approach used in ideal, free models, but in the case of flocks the model must be constrained by the cost of vigilance. This approach should be generally applicable to the case of geese, as well as to other herbivorous species which possess the essential characteristics of a high, perceived predation risk and a preference for abundant, immobile prey.

The aggregation of individuals in flocks can be seen as the result of a fitness function which is domed in relation to flock size (Fig. 1). In small flocks, time spent feeding is reduced by increased vigilance, while in large flocks, intake rate is reduced as a result of resource depletion. However, depletion does not affect all individuals

equally. In the case of barnacle geese, depletion is more severe in the centre of flocks. Individuals which feed in this position therefore suffer more from the presence of competitors than those which occupy the edge (Black & Owen 1989a; Black et al. 1992). Thus, if we are to construct a model which simulates the intake rates achieved by the members of a goose population, we need to understand the processes which determine the distribution of individuals not only between but also within flocks.

Evidence from flock behaviour suggests that sub-dominant individuals lose little time to aggressive encounters at the edge of flocks, where potential intake rate is highest, while dominant individuals conversely spend considerable time engaged in aggression (Black & Owen 1989a; Black et al. 1992). This is because sub-dominant individuals tend to simply move away from aggressive, dominant birds with little interruption of feeding, rather than attempting to defend themselves (Black & Owen 1984; Siriwardena & Black in press). Within-flock distribution is thus clearly not tractable in terms of an ideal, free distribution, in which sub-dominant individuals would avoid the best part of the flock because interference reduces intake rate. Within-flock distribution can rather be seen as a form of despotic distribution, in which dominant individuals physically exclude sub-dominants. Flock position can therefore be seen as directly related to dominance rank—the most dominant individuals occupy the best positions, middle ranking individuals occupy flock areas with intermediate profitability, and the lowest ranking individuals occupy the least profitable parts (Black & Owen 1989a).

Model structure

The model groups individuals into functional units: unpaired individuals, pairs without goslings, and families with varying numbers of goslings. For a given proportion of juveniles in the population, the distribution of family sizes is assumed to follow a Poisson distribution. Each functional unit is assigned a unique dominance rank based on the number of individual members present. Dominance rank determines the position that a unit can attain within flocks. A number of patches with differing available biomass are provided in the model. Units choose among these patches sequen-

tially in a random order, selecting the patch which provides the maximum intake rate at the time of choosing. A single iteration allows every unit one chance to move, and iterations are carried out until no further movement is possible.

Achievable intake rate is calculated on the basis of the trade-off between lost feeding time and depletion. The relationship between proportion of time spent feeding (f) and flock size (N) takes a capped linear form, with a constant value (f_{\max}) above a certain threshold flock size (N_t):

$$f = \begin{cases} f_{\min} + \frac{N(f_{\max} - f_{\min})}{N_t} & \text{if } N < N_t \\ f_{\max} & \text{if } N \geq N_t \end{cases} \quad (1)$$

The intake rate (k) achieved by an individual presented with a given food biomass (B) is determined by an asymptotic functional response, modelled using Holling's (1959) equation,

$$k = \frac{aB}{1 + ahB} \quad (2)$$

in which the parameter a determines the rate of biomass removal at biomass levels approaching zero, and h determines the maximum asymptotic rate of removal at high biomass. In this case, intake is defined in general terms, making no assumptions about the relative importance of quality and quantity. For the purposes of the theoretical exploration presented here, the total available resource may be envisaged either as actual biomass or some composite of quantity and quality such as the total amount of metabolisable energy available.

The amount of depletion experienced by a given individual is determined as the total intake of all the individuals between it and the edge of the flock. Within-flock distribution is assumed to follow the despotic model (see above) which is based on dominance rank. The model therefore packs functional units into flocks sequentially according to their dominance score. The most dominant individuals fill the outer edge of the flock first, with lower ranking individuals sequentially filling the inner layers. As a simplification for the purposes of initial model exploration, it was assumed that flocks are circular, allowing the number (n) with a given number of preceding competitors (d) in a flock of a given size (N) to be calculated from

$$n = \pi \left(2\sqrt{N/\pi} - 2d - 1 \right) \quad (3)$$

Model output

The purpose of the model explorations presented here is to provide insight into the workings of the model rather than to make accurate predictions. The explorations give predicted flock sizes and intake rates achieved for a single hypothetical point in time using non-specific parameters.

The predicted distribution of individuals was unstable, never converging on a state where no unit could improve its intake rate by moving. This phenomenon also occurs in ideal, free models of distribution incorporating kleptoparasitism (Parker & Sutherland 1986). Such kleptoparasitic models are similar to the flock model presented here in that some individuals suffer from the presence of conspecifics while others gain. The predicted distribution of individuals was readily stabilised by incorporating a perceptual constraint. Using this method, units only change patches if the proportional increase in intake rate thus achieved is greater than a small, arbitrary amount. The median and range of flock sizes and intake rates achieved by all functional units in the population are obtained for the point at which the distribution has stabilised, and there are therefore no further improvements in foraging performance possible for any individual.

The sensitivity of average instantaneous intake rate achieved to total population size was low (Fig. 2A) because increasing total population tends to result in the formation of more flocks of similar size rather than increased flock size (Fig. 2B). In addition, differences in patch profitability were low in this simulation, meaning that intake rate in a given flock position varied little between the best and worst occupied patches. Note, however, that although average intake rates are hardly affected, the intake rate achieved by the least dominant did show a substantial decline with increasing population size. Average flock size was considerably greater than the threshold level above which there is no further improvement in feeding time (500). This supports the observation of Sibly (1983) that stable group size is, in theory, likely to be larger than the optimum group size. Although instantaneous intake was insensitive to population size, individual performance over a whole season is likely to be more sensitive because the effects of depletion accumulate over a long time span.

Contrasted with the effects of population size, the proportion of the available food taken by each

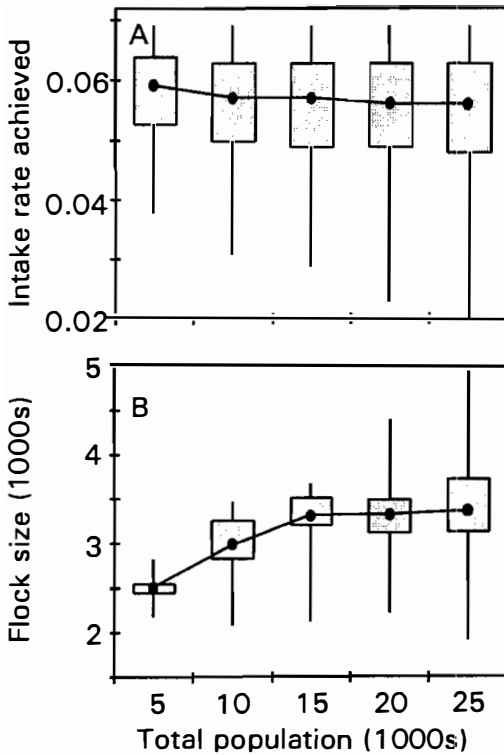


Fig. 2. The sensitivity of (A) achieved intake rate (defined as a proportion of the available resource) and (B) flock size to total population size. Points are medians, boxes indicate the interquartile range (containing the central 50% of the population) and whiskers indicate the total range.

individual had a strong effect both on realised intake rates and on flock sizes (Fig. 3). As individuals took an increasing proportion of the available food, less remained for the lower ranking individuals resulting in a greater disparity in foraging performance between high and low-ranking individuals. At low individual depletion rates, there was virtually no difference. As a result, the entire population was predicted to choose the best patch.

Future directions

Work is currently underway to parameterise the model, using data on the observed dynamics of flocks and the behaviour of individuals within

flocks. Following this, the predictions of the model will be validated by comparing predicted patterns with those observed over the winter. In particular, the success of the model may be judged by how well predicted patterns of field use, flock size and resource acquisition by different social classes match those observed. The modelling process will then proceed by exploring the consequences of changing resource levels, population sizes and weather conditions for overwinter mortality patterns. This procedure will then be integrated into a behaviour-based model of the annual cycle, which will include separate models for foraging performance on the breeding and staging grounds.

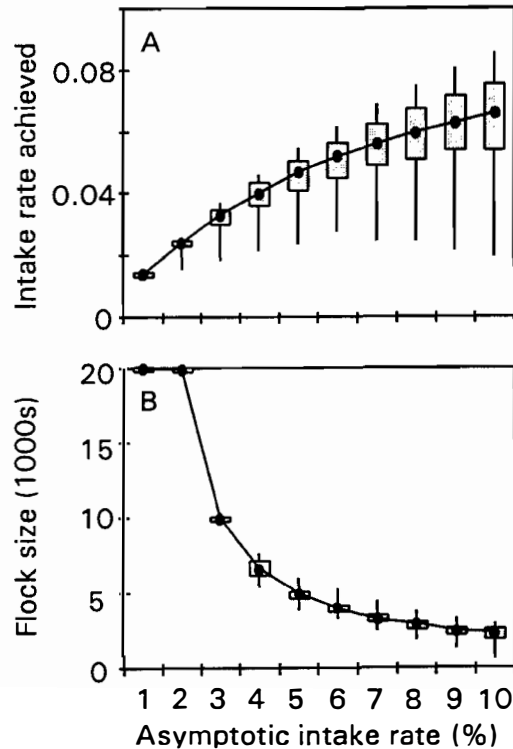


Fig. 3. The sensitivity of (A) achieved intake rate (defined as a proportion of the available resource) and (B) flock size to individual depletion rate. Asymptotic intake rate is defined as the asymptote of the functional response (Eq. 2), expressed as a percentage of the available biomass consumed. Points are medians, boxes indicate the inter-quartile range (containing the central 50% of the population) and whiskers indicate the total range. A total population of 20,000 is simulated.

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From individual feeding performance to predicting population dynamics in barnacle geese: The spring staging model

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Lang, A., Houston, A. I., Black, J. M., Pettifor, R. A. & Prop, J. 1998: From individual feeding performance to predicting population dynamics in barnacle geese: The spring staging model. Pp. 203–211 in Mehlum, F., Black, J. M., Madsen, J. (eds.): Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skrifter* 200.

We present an individuals-based simulation model that predicts changes in energetic reserve levels for barnacle geese *Branta leucopsis* during spring staging on the archipelago of Helgeland, Norway. We assume a despotic distribution of geese foraging on small patches of vegetation with the best competitors foraging on the patches that offer the highest daily intake rate and biomass. Competitive ability in the model increases with age, past reproductive success and previous residency on an archipelago. Intake rates and energetic reserves are calculated on a daily basis. There are two traditional archipelago types included in the model (managed and unmanaged) and three classes of vegetation (*Festuca*, Herb and Hay meadows). The Hay meadow is a result of the application of fertilisers and grazing and is therefore only present on the managed archipelago. Our model explores the effect of food availability on an archipelago of each type at different population densities. At high goose densities there is a marked reduction in the intake rates of poor competitors. This effect is stronger on the unmanaged archipelago where there is no Hay meadow. We then consider how this basic model could be improved with further parameterisation.

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Introduction

In order to model the dynamics of a population, we must be able to describe how the density of the population affects the survival and reproductive success of its members. The main period of adult mortality in the Svalbard population of barnacle geese *Branta leucopsis* is during the autumn migration, presumably because of insufficient energy reserves (Owen & Black 1989; 1991). In addition, the primary determinants of the reproductive success of arctic breeding geese are considered to be the level of reserves that female geese have at the start of the breeding season and the timing of nest initiation (Ankney & MacInnes

1978; Ebbinge 1989; Hamman & Cooke 1989). It should therefore be possible to predict the survival and reproductive success of the population by modelling the changes in energetic reserves, as a consequence of foraging and energy expenditure, through the annual cycle. For the population as a whole, the average foraging performance of the geese will be determined by the amount and quality of food available in each habitat accessible to the population. However, when geese compete for food, some individuals are able to gain access to the best feeding sites and thus increase their level of reserves more rapidly than others (Teunissen et al. 1985; Prop & Loonen 1988; Black & Owen 1989a, b; Black et al. 1991, 1992; Mulder et al. 1995). Here we predict the rate of

change of reserves for each individual in two model populations during the spring staging period on the coast of Norway.

Background

Each spring, Svalbard barnacle geese migrate from Scotland to the breeding areas on Svalbard, staging on Helgeland off the coast of Norway. Helgeland is composed of many small archipelagos. Traditionally, the geese have used small archipelagos away from the mainland. Some of these archipelagos have been managed for livestock whilst others remain unmanaged. Vegetation and goose foraging has been studied on both types of archipelagos (Black *et al.* 1991; Prop & Black 1998, this volume; Prop *et al.* 1998). Around the rocky shores of all archipelagos there is a zone of salt-tolerant *Festuca rubra*, and inland there are Herb meadows that consist of several herb and some *Poa* species. Because of their low grass content, the Herb meadows offer little food for geese. In contrast, on the managed islands there are also Hay meadows with *Festuca rubra* and several *Poa* species. The vegetation is quite sparse on these archipelagos and the geese typically forage in pairs within small loose flocks (Black *et al.* 1991). Evidence suggests that the geese are competing for patches of high quality vegetation

(Black & Prop unpubl. data). Variation in access to high quality patches results in variation between individuals' intake rates. Access to the best foraging areas can be gained through food-finding skills enhanced by previous knowledge of the foraging areas and through aggressive encounters between geese in which dominant pairs exclude others from feeding areas (Prop & Black unpubl. data). The differences in intake rates result in differences in energetic reserve levels, which are observed as differences in abdominal profiles. Older geese and geese that are foraging in the same area used in previous years typically show a more rapid increase in abdominal profiles than younger geese (Prop & Black unpubl. data).

The modelling approach

In the spring stage of the annual cycle, we assume that all geese are in pairs. Although the vegetation classes are described as meadows, the vegetation is very patchy. The spring model is based on the assumptions that patches of vegetation can be defended by a single pair of geese and that the geese that are good competitors feed in the patches that provide the highest daily intake. That is, we assume that there is a despotic distribution of pairs of geese (Fretwell & Lucas 1970; Sutherland 1997). The model is summarised in Fig. 1.

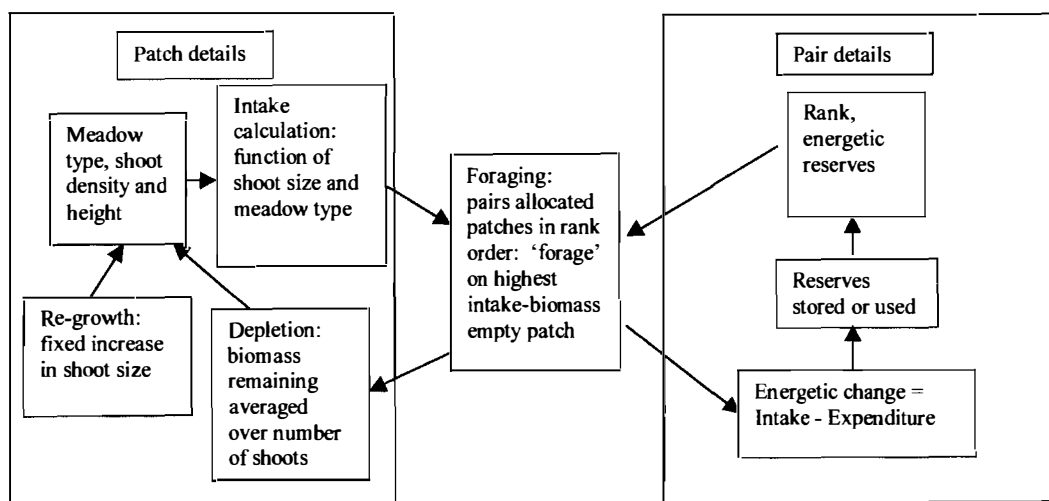


Fig. 1. Model summary.

The vegetation

The two archipelago types, managed and unmanaged, are modelled separately with the geese being allowed to move freely around on archipelagos of the same type. The total area of each archipelago type is then subdivided into classes by the percentage of vegetation type covering the area, and each vegetation class is divided into patches of a given area. The patch size is chosen so that no pair consumes all the biomass of a patch in a day. In the examples presented, a patch size of 12 m² is used (note that reducing the patch size and increasing the number of iterations in a day had little effect). The shoot density of each patch is drawn from an approximated Poisson distribution and the initial shoot size is taken from a Normal distribution. Each day the shoot size and biomass of each patch are recalculated to allow for any depletion and re-growth.

The geese

On arrival, the competitive ability of each pair of geese is calculated relative to the other pairs on the same archipelago type. Because marked pairs are observed feeding in the same areas throughout the spring, we assume there is no switching between archipelagos (Black et al. 1991). The competitive ability of a pair is a rank score based on age, past reproductive success and previous residency. The best competitor on each archipelago is ranked 1. Each day the pairs present are allocated patches in rank order. A pair chooses the unoccupied patch on the appropriate archipelago type that offers the highest daily intake based on shoot size and vegetation class, provided there is sufficient biomass to supply the intake for the whole day. If two patches offer the same intake rates, the pair chooses the unoccupied patch with the highest biomass. This decision rule has no specific observational support but seems reasonable. The intake (mg dry weight) is translated into metabolisable energy. If the daily intake exceeds the daily energetic requirements, the excess is stored. If the intake is below the daily energetic requirement, then stored reserves are used to make up the difference. If the stored reserves fall below zero, the pair dies.

Table 1. Percentage cover of the main vegetation classes

	<i>Festuca</i>	Hay	Herb
Managed	10	15	10
Unmanaged	15	0	25

Parameters

Foraging parameters used in the model are from data gathered in 1990–1992 on Helgeland (Prop & Black 1998, this volume; Prop et al. 1998). We use data from the managed archipelago of Sandvær and the unmanaged archipelago of Laanan. The unmanaged archipelagos have a large area of Herb meadow and no Hay meadow so the total biomass available is lowest on this archipelago type. In addition, the intake rate is lowest on the Herb meadows. Therefore, we expect the unmanaged archipelagos to provide a poorer habitat for foraging geese. The parameters used are (i) proportion of cover of each vegetation class used by the geese for each archipelago type (Table 1); (ii) shoot density of each vegetation class, using square root-transformed data (Table 2); (iii) intake rate as a function of shoot size for each meadow type; (iv) initial shoot size on 1 May: mean, 35 mm, and standard deviation, 11 mm; (v) daily shoot growth rate of 1 mm; and (vi) shoot weight 0.04 mg/mm. Note that the proportion cover combines data for Home islands and Outer islands assuming Laanan Home island (unmanaged) is 10 ha. and Sandvær Home island (managed) is 30 ha.

Metabolic parameters were either estimated from feeding trials on brent geese and scaled up (Prop unpubl.) or were taken from the literature. Parameters used are (i) food processing rate of barnacle goose: 78.9 g wet weight/h, assuming 75% water equals 19.23 g dry weight/h; (ii) Helgeland daily energy requirements 1200 kJ; (iii) metabolisable energy Helgeland grasses 7.11 kJ/g dry weight (Prop & Vulink 1992); (iv)

Table 2. Distribution of shoot densities for the main vegetation classes

shoots m ⁻²	<i>Festuca</i>	Hay	Herb
mean	9801	6084	2025
s.d.	441	225	484

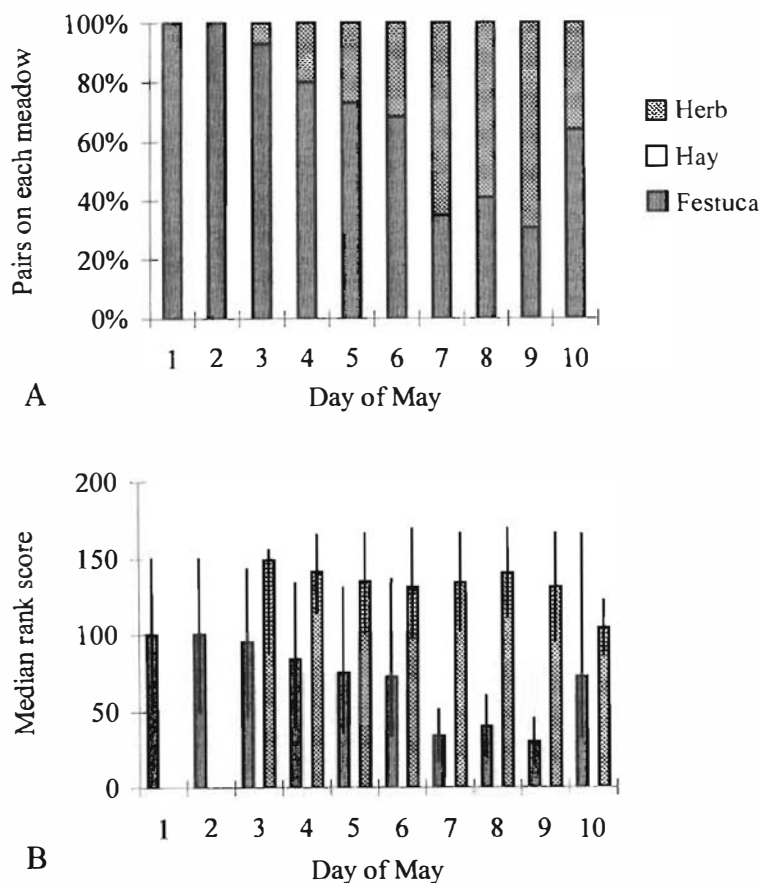


Fig. 2. Distribution of pairs on each meadow at a population size of 200 pairs. A. Numbers of pairs. B. Median rank scores with bars indicating upper and lower quartiles for unmanaged archipelagos.

daylight 19 h; and (v) Energy storage efficiency 70% and reserve use efficiency 77% (Bromley & Jarvis 1993).

population sizes of 200 and 400 pairs on each archipelago.

Low numbers

Results from the model

As an illustration, we consider 100 hectares of unmanaged archipelago and 100 hectares of managed archipelago. The initial average shoot size of all meadows is the same on 1 May and the grass growth is constant each day. All the geese arrive on the same day, 1 May, and we run the model for 10 days. Analyses were performed for a range of parameters. The model was primarily sensitive to grass growth rate. Below we present results for the best estimates of the parameters for

When there are only 200 pairs of geese on each archipelago, all pairs achieve the maximum intake rate possible, limited only by their food processing rate. Their choice of patch is, therefore, purely based on biomass. On the unmanaged archipelago all pairs feed on the *Festuca* meadows for the first 2 days (Fig. 2A). During these days, the median biomass of both meadows increases slowly as the geese feed on biomass which was produced before they arrived. However, the growth rate of the *Festuca* meadows is lower than the depletion rate; thus, from day 3 the median biomass of the *Festuca* meadows decreases. In contrast, the Herb

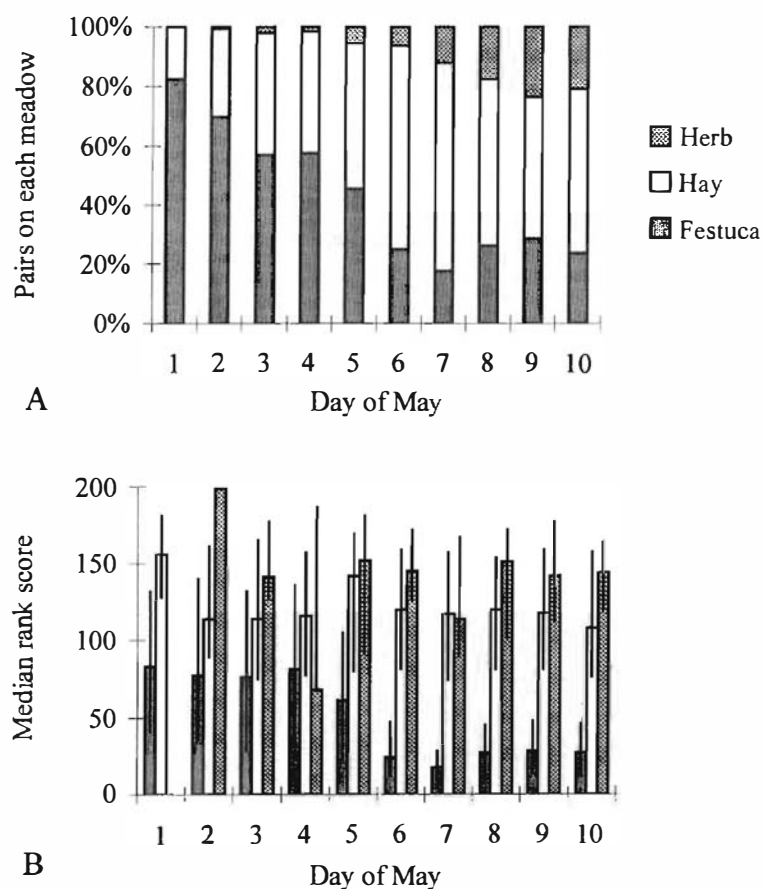


Fig. 3. Distribution of pairs on each meadow at a population size of 200 pairs. A. Numbers of pairs. B. Median rank scores with bars indicating upper and lower quartiles for managed archipelagos.

meadows suffer no depletion and by day 3 some patches of the Herb meadow contain higher biomass than the poorest *Festuca* meadows. We then see a few pairs of geese switch from the *Festuca* meadows to the Herb meadows. The median rank score of the pairs that switch is higher than that of the pairs that remain on the *Festuca* meadow (Fig. 2B). It is not, however, the very poorest competitors which switch to the Herb meadows. This is because only the patches of the Herb meadow with extremely high values of biomass are better than the poorest *Festuca* meadow patches. As the *Festuca* meadows are further depleted, more pairs of geese switch to the Herb meadows. By day 7, only a third of the pairs remain on the *Festuca* meadows, and these are clearly the pairs with the lowest rank score, i.e. the best competitors (Fig. 2B). Because of the very low shoot density of grasses on the Herb meadows,

the high level of grazing causes a marked reduction in median biomass and by day 10 many of the poorer competitors have switched back to the *Festuca* meadows.

On the managed archipelago there is more overlap in the ranges of the patch biomass available on each meadow type. In particular, the upper quartile of the patch biomass of the Hay meadow overlaps with the lower quartile of the *Festuca* meadow. This results in a small number of pairs of geese feeding on the Hay meadows from day 1. By day 2 a few patches of the Herb meadows are also used and on day 7 the majority of pairs are feeding on the Hay meadows (Fig. 3A and B). As the Hay and Herb meadows become depleted, however, pairs move back to the *Festuca* meadows. In general the median rank score on each meadow reflects the median biomass available on the meadow. Thus the competitive ability

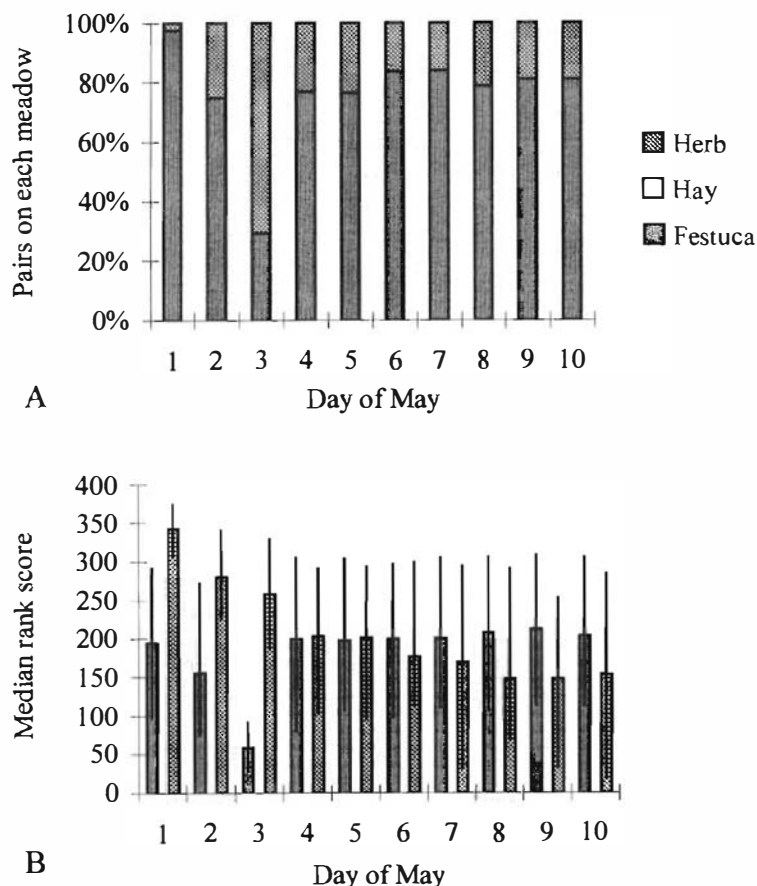


Fig. 4. Distribution of pairs on each meadow at a population size of 400 pairs. A. Numbers of pairs. B. Median rank scores with bars indicating upper and lower quartiles for unmanaged archipelagos.

of geese on the *Festuca* meadows are usually higher than that of the Hay meadows, which in turn is higher than that of the Herb meadows.

High numbers

When there are 400 pairs on each archipelago, the pattern of meadow use is similar to the pattern described above. However, switching from the *Festuca* meadow occurs earlier because of the increased depletion rate. The switch back to *Festuca* also occurs earlier (Figs. 4A and 5A). The effect of this high level of depletion is a continual decrease in the biomass of all meadow types from day 5. From day 6 the distribution of pairs appears to stabilise both in terms of numbers and rank scores (Figs. 4B and 5B). The numbers of pairs on each meadow reflect the biomass avail-

able on each meadow. However, the rank scores indicate that the herb meadow provides a few patches of very high biomass and shoot size that are used by the pairs with the lowest rank score (the best competitors).

Once the population reaches 400 pairs on each archipelago, we begin to see effects of goose density on the intake rates of the geese. Fig. 6A illustrates the decrease in intake rate observed on both archipelagos. For the first three days all pairs of geese achieve the maximum daily intake. The best competitors (ranked 1) continue to achieve this high intake throughout the 10 days. The intake of poorer competitors falls steadily each day. The effect of depletion is less marked on the managed archipelago than on the unmanaged archipelago. On the unmanaged archipelago the intake of the pair of geese ranked 25 is similar to that of the pair ranked 200 on the managed archipelago on days 4 and 5. The daily intake of poorer competitors then

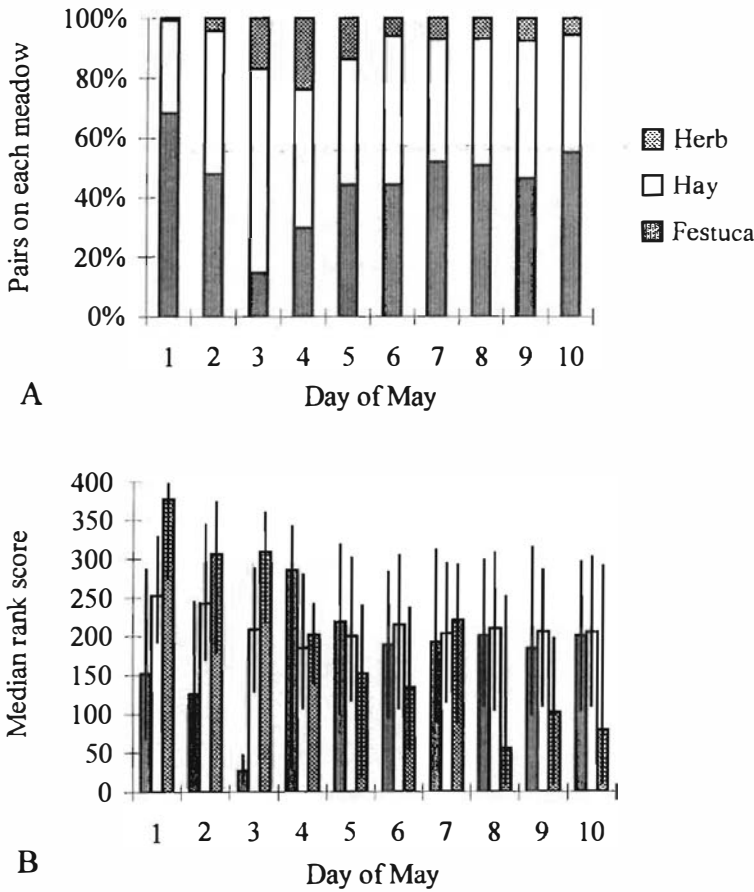


Fig. 5. Distribution of pairs on each meadow at a population size of 400 pairs. A. Numbers of pairs. B. Median rank scores with bars indicating upper and lower quartiles for managed archipelagos.

decreases more sharply so that by day 10 the pair ranked 25 on the unmanaged archipelago only achieve a daily intake similar to that of the pair ranked 400 on the managed archipelago. Fig. 6B shows the impact of the reduced intake rates on reserve levels. Over the 10 days the increase in reserves of the pair ranked 400 on the unmanaged archipelago is approximately 40% less than that of the pairs ranked 1 on both archipelagos.

Discussion

The model for the foraging of barnacle geese on the spring staging areas of Helgeland is based on the assumptions that pairs of geese compete for patches of vegetation and that the best competitors will gain access to the highest quality patches. In

this context the highest quality patch is that which offers the highest intake rate and the highest biomass. When the daily foraging decisions of the simulated pairs of geese occur in conformity with these assumptions, relatively complex patterns of habitat use result on both types of archipelagos modelled.

When the daily intake rates of the geese are limited solely by food processing rate, the geese choose where to forage purely on the biomass available in each patch. The result is that at low population densities the good competitors feed on the *Festuca* meadows because these meadows contain the patches with the highest shoot densities. As the *Festuca* meadows are depleted, poor competitors on the unmanaged archipelago switch to the Herb meadow, whereas poor competitors on the managed archipelagos switch to the Hay meadow. As the population density increases, switching from *Festuca* meadows

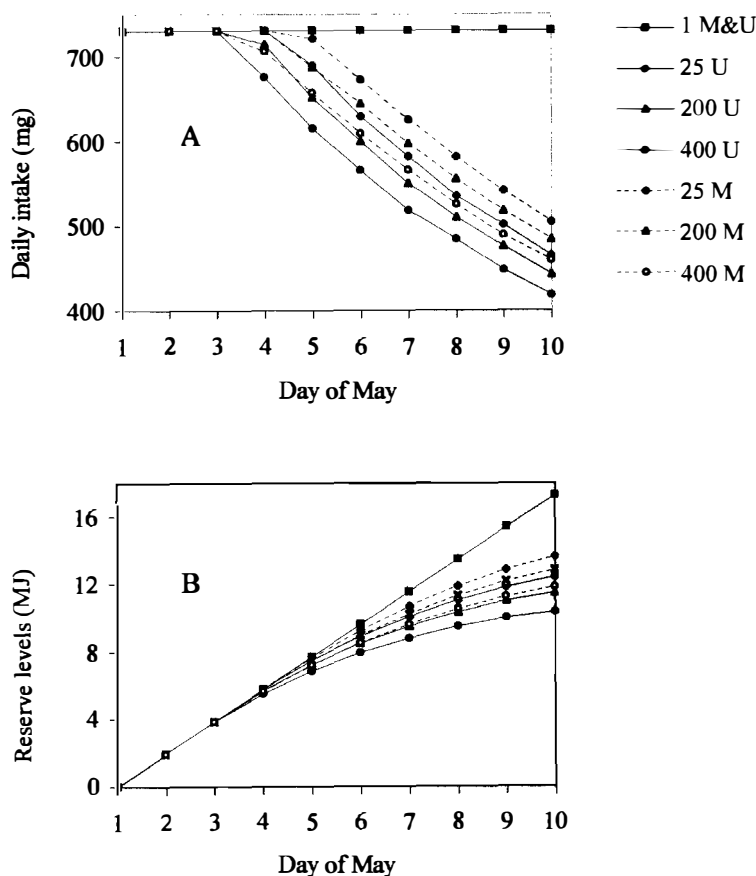


Fig. 6. Intake rates (A) and reserve levels (B) for selected pairs on the managed (M) and unmanaged (U) archipelagos. Pairs ranked 1, 25, 200 and 400 are included.

occurs earlier. The Hay meadow on the managed archipelago is slowly depleted and towards the end of the period, pairs switch to the Herb meadow and back on to the *Festuca* meadow. The Herb meadows on both archipelagos are rapidly depleted because the average shoot density is very low. Therefore, there is only a short period when a high proportion of either population uses the Herb meadows. At high population densities the numbers exploiting each meadow type stabilises rapidly.

The effect of depletion on intake rates and hence on changes in reserves is only visible at high population densities. The best competitors on each archipelago achieve maximum intake rates throughout the period, and thus their reserve levels increase linearly. Because poorer competitors cannot gain access to the most profitable patches, their intake rates are most affected by competition, and their reserve levels increase very slowly

towards the end of the foraging period. The effect of depletion on poor competitors is more severe on the unmanaged archipelago than on the managed archipelago because the total area of *Festuca* and Hay meadow on the managed archipelago is greater than that of the *Festuca* meadow on the unmanaged archipelago. As these meadows are much more productive than the Herb meadows, the total production of biomass is lower on the unmanaged archipelago.

This model of despotic foraging has allowed us to explore the potential importance of the availability of food at different population densities for Svalbard barnacle geese during the spring staging phase of their annual cycle. We have shown that variation in competitive ability of barnacle geese and food availability of their habitat can be linked to foraging performance and grazing pressure. The next stage in the development of this foraging model is to incorporate more detail in the grass

sub-model. The most obvious amendment is to incorporate temperature-dependent grass growth. Slow grass growth in late April and early May because of low temperatures can have serious effects on the initial biomass available to the geese (Prop et al. in press). Additionally, the protein content of the grasses used by the geese has been shown to change through May (Black et al. 1991; Prop & Black 1998, this volume). Incorporating a decline in protein is likely to further alter the rate of increase of energetic reserve levels that the current model predicts.

The model will ultimately be incorporated into a year-round model that will predict survival and reproductive success for the population of Svalbard barnacle geese. We can then investigate the population dynamics under a range of environmental conditions and explore potential effects of management policies that have been planned for this population (Black 1998, this volume).

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Continuing growth of the Baltic barnacle goose population: Number of individuals and reproductive success in different colonies

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Larsson, K. & van der Jeugd, H. P. 1998: Continuing growth of the Baltic barnacle goose population: Number of individuals and reproductive success in different colonies. Pp. 213–219 in Mehlum, F., Black, J. M. & Madsen, J. (eds.): Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skrifter* 200.

The Baltic barnacle goose population increased rapidly after 1971, when the first breeding attempt was observed off the eastern coast of Gotland, Sweden. In 1997, about 3,990 pairs bred along the Baltic coast in Sweden, western Estonia and southern Finland. The majority of these pairs, about 3,490 pairs, were found breeding in colonies along the eastern coasts of Gotland and Öland, Sweden. The total population size at the end of July in 1997 was estimated to be approximately 17,000 individuals. The production of fledged young per breeding pair was negatively related to the size of colonies, although the production varied greatly among different colonies. In 1997, the largest Baltic colony hosted more than 50% of the total number of breeding pairs but produced less than 15% of the total number of fledged young. This finding points out the need to consider different colonies as separate demographic units when studying regulation processes in populations of colonially breeding geese. In the future, we find it most probable that the Baltic population will continue to increase and that new colonies will be established. We also expect that the number of Baltic barnacle geese eventually will be limited by the availability of predator-safe grazing grounds with short, protein rich grass which families with newly hatched goslings are dependent on.

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Introduction

Barnacle geese were first observed breeding in the Baltic area in 1971 (Larsson et al. 1988). However, barnacle geese belonging to the Russian population have for at least a century used the coastal areas around the Baltic Sea, including the present breeding sites, as staging areas in spring and autumn on their migration to and from their arctic breeding grounds (Wibeck 1946; Kumari 1971; Ganter et al. 1999). It is therefore likely that the first Baltic breeding barnacle geese originated from the Arctic Russian barnacle goose population (Larsson et al. 1988). Since the spontaneous establishment in the Baltic area in 1971, the number of breeding barnacle geese has increased rapidly. At present, most breeding pairs can be found in colonies along the eastern coast of the islands of Gotland and Öland, Sweden (Larsson & Forslund 1994). Solitary breeding pairs and small colonies have also been found in western Estonia around the islands of Saaremaa and Hiiumaa

(Leito 1996), in southern Finland (Laine 1996), and along the coast of mainland Sweden (SOF 1993, 1994, 1995, 1996, 1997; Lindborg 1997). Some of the birds which have been observed breeding in Finland and along the coast of mainland Sweden are known to have originated from captive populations (Laine 1996; SOF 1995). A small number of barnacle geese have also recently been found breeding in Denmark and in the Netherlands (Meininger & van Swelm 1994; Ganter et al. 1999; K. Koffijberg pers. comm. 1997). The birds belonging to the Baltic and Arctic Russian populations mix on the wintering grounds in The Netherlands and Germany.

Several of the Baltic barnacle goose colonies have been the subject of detailed ecological research. Information on the number of breeding pairs in some of the colonies as well as data on reproductive success and survival of individually marked birds has therefore been published previously (see for example Larsson et al. 1988, 1998; Forslund & Larsson 1991a, b, 1992; Larsson & Forslund 1994; Leito 1996, van der Jeugd &

Larsson 1998). The aim of this paper is to bring together the already published, and the most recently unpublished, information about the number of breeding barnacle geese in the Baltic area. In addition, we present information about the production of fledged young in different colonies as well as an estimate of the total number of individuals in the Baltic population.

Methods

Number of breeding pairs and fledged young

Counts of breeding pairs have been performed yearly in most of the larger Baltic colonies. In most years the number of breeding pairs has been estimated from nest counts in mid-May. Before 1984, and later also in some of the small colonies, direct nest counts could not be performed. In these years the number of breeding pairs were estimated from counts of families with newly hatched young. Because few birds were breeding in the Baltic before 1984 and losses during incubation are relatively rare, the latter method to estimate the number of breeding pairs can also be regarded as accurate. For more information about the methods used in specific years and sites we refer to Larsson & Forslund (1994), Laine (1996), Leito (1996) and Lindborg (1997). Estimates of the number of breeding pairs in the six largest colonies in the most recent years, i.e. data which have not been previously published, are all obtained from direct nest counts.

In mid-July, one to two weeks before the young fledge, brood sizes of marked pairs and/or the total number of young were counted on grazing sites close to the colonies on Gotland and Öland. Because the mortality of young is low at that time of year, the yearly production of fledged young in the different colonies could be calculated from the brood size counts or the total counts of young (Larsson & Forslund 1994).

Total number of individuals

No attempts have hitherto been made to directly count the total number of individuals in the Baltic

barnacle goose population. The reason for this is that birds from the Baltic population are partly or completely mixed with birds from the Russian population from the end of September to the middle of May. However, in May and at the beginning of June, breeding Baltic barnacle geese are found within the colonies and the number of breeding individuals can be estimated as twice the number of observed nests. In the middle or end of July, it is also possible to directly count the number of fledged young because family groups are usually concentrated at relatively few grazing sites within a distance of about 30 km from the colonies. However, during summer non-breeding barnacle geese are distributed in small groups over large areas which makes it very difficult to perform direct counts. To obtain an estimate of the total number of individuals belonging to the Baltic population, it is therefore necessary to first estimate the number of non-breeding individuals present. Such an estimate can be obtained by combining information about the number of fledged young in earlier years, the age-specific survival rates and the proportion of birds that breed at different ages. Estimates of yearly survival rates from fledging and onwards are available from analyses of more than 45,000 winter resightings of about 1,300 fledged young colour-ringed at the largest Baltic colony (van der Jeugd & Larsson 1998). Estimates of yearly survival rates of older birds can be obtained from analyses of resightings of about 3,000 birds marked as juveniles or adults in the largest colony (Larsson et al. 1998). Estimates of the proportion of birds that start breeding at different ages are also available from analyses of barnacle geese ringed in the largest Baltic colony. Although some birds start breeding when two years old, it has been found that a considerable proportion of the young geese do not start breeding until they are three or four years old (Larsson 1992; van der Jeugd & Larsson unpubl.).

Results

Number of breeding pairs

The number of breeding pairs in the six largest colonies on Gotland and Öland has increased rapidly since colony establishment (Figs. 1 and 2).

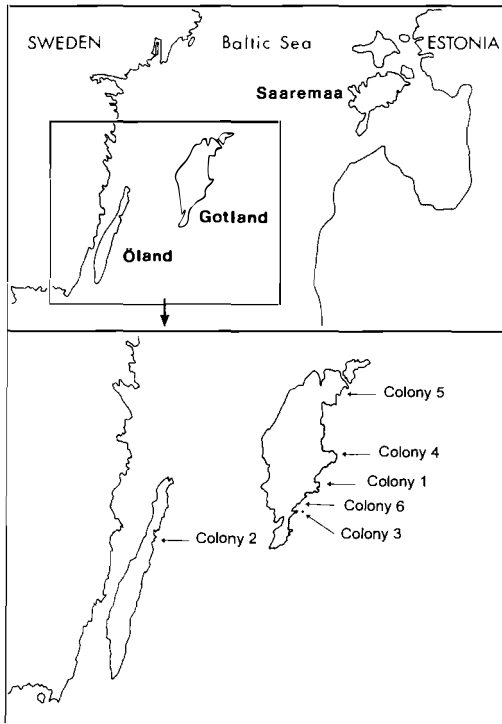


Fig. 1. Map showing the location of the six largest barnacle goose colonies on Gotland and Öland, Sweden. The six colonies are situated on the following islands: (1) Laus holmar, (2) Kåreholm, Sillgrund, Villgrund, (3) Rone Ytterholme, Koggen, (4) Östergarnsholm, (5) Skenholmen, (6) Sigdesholmen, Getorskär, Petsarvegrunn.

In colony 1, which is the oldest Baltic colony, the rate of increase of the number of breeding pairs was approximately 54% per year during the first 15 years after the colony was established. Thereafter, the rate of increase levelled off to approximately 12% per year because of density-dependent effects on reproduction (Larsson & Forslund 1994). The rate of increase in the younger colonies, i.e. in colonies 2 to 6 on Gotland and Öland, was comparable to, or even higher, than the early rate of increase in colony 1 (Fig. 2). In colony 5, the number of nests showed a sudden decrease between 1996 and 1997. The few nests that were found in 1997 also contained very few eggs. This decrease in number of nests and eggs was due to predation by several red foxes *Vulpes vulpes* which probably reached the island during the winter of 1996/97 and spent most of the summer of 1997 on the breeding island. In colony 6 the first observations of breeding birds are from 1995.

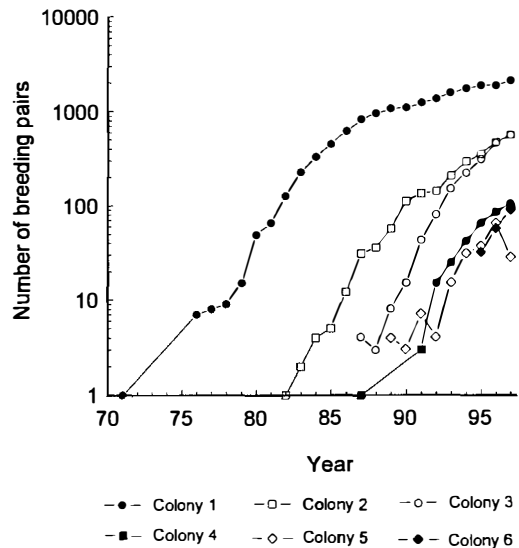


Fig. 2. Number of breeding pairs in the six main barnacle goose colonies on Gotland and Öland, Sweden, since 1971. Data is mainly obtained from Larsson et al. 1988 and Larsson & Forslund 1994.

However, it is very likely that a small number of birds had bred at that site also in some earlier years. A small number of birds is also known to have bred outside the six main colonies on Gotland and Öland during the 1980s and 1990s. In 1997, approximately 20 pairs bred at other sites on Gotland and Öland. In total, approximately 3,490 pairs were breeding on Gotland and Öland in 1997.

The number of breeding barnacle geese has also increased at several other sites in the Baltic region, such as in western Estonia and along the coasts of Sweden and southern Finland (Fig. 3). The presented figures are the observed total numbers of pairs breeding solitary and in small colonies. In Estonia and Finland, barnacle geese have been found breeding at at least 13 and 18 different sites, respectively (Laine 1996; Leito 1996). In 1996 and 1997, all breeding sites were not visited in Estonia and Finland. The figures given for these years should therefore be regarded as minimum figures (A. Leito pers. comm. 1997; J. Laine pers. comm. 1997).

In Sweden, a small number of free-flying birds have been breeding within the zoological garden of Skansen, Stockholm, since the 1970s. Since the end of the 1980s, barnacle geese have also started to breed in increasing numbers outside Skansen on various islands within the city of Stockholm

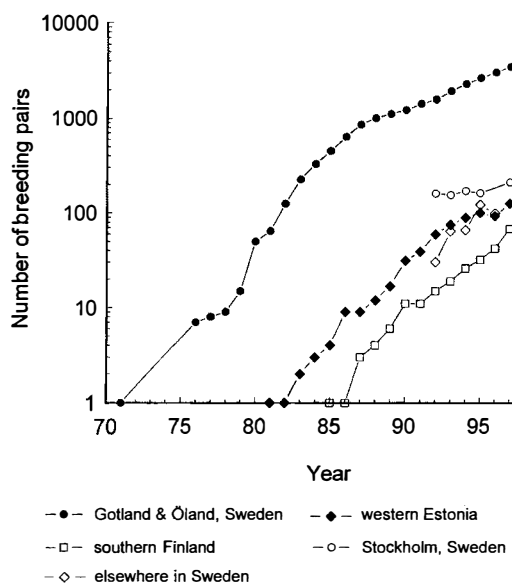


Fig. 3. Number of breeding pairs in barnacle goose colonies situated on Gotland and Öland, in western Estonia, southern Finland, Stockholm (including Skansen), and elsewhere in Sweden since 1971. Data is obtained from SOF (1993, 1994, 1995, 1996, 1997), Leito (1996), Laine (1996), Lindborg (1997), A. Leito, pers. comm. 1997, J. Laine pers. comm. 1997, T. Lindborg pers. comm. 1997. In 1996 and 1997 the figures given for western Estonia and southern Finland are minimum figures because not all previously known breeding sites were visited in these years.

(Lindborg 1997; T. Lindborg pers. comm. 1997) (Fig. 3). It is assumed that these latter colonies were founded by birds from the semi-captive Skansen population. In recent years, barnacle geese have also been found breeding in small numbers at a large number of sites along the coast of mainland Sweden. A part of these birds probably originate from captive populations.

Although barnacle geese have been found breeding in increasing numbers at a large number of sites in the Baltic region, it should be noted that the vast majority of the Baltic-breeding barnacle geese, approximately 87% in 1997, were breeding in the six largest colonies on Gotland and Öland (Fig. 3). In total, approximately 3,990 pairs were breeding in the Baltic area in 1997.

Number of fledged young

The production of fledged young in the six main

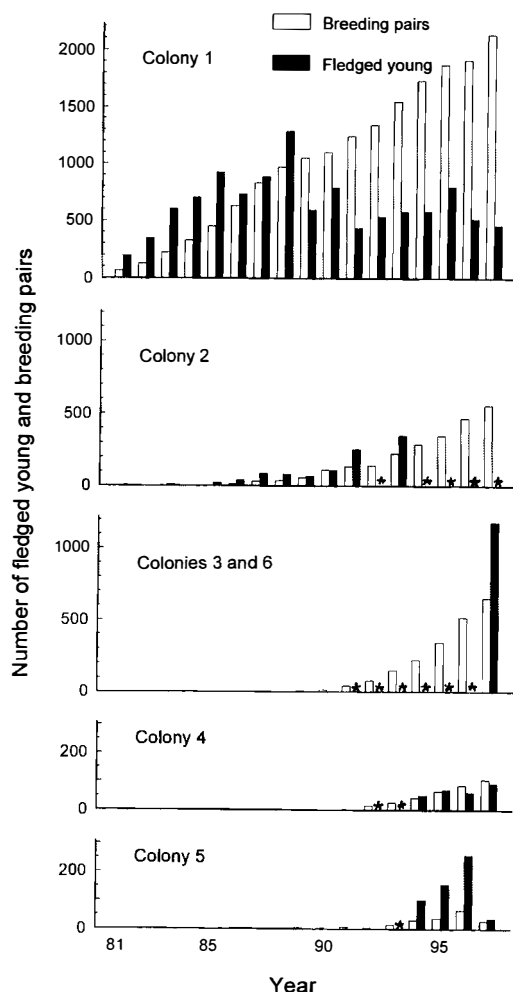


Fig. 4. Total production of fledged young in six barnacle goose colonies on Gotland and Öland since 1981. Asterisks indicate that data on number of fledged young are missing. Note that colony 3 and 6 which in 1997 together consisted of about 650 breeding pairs produced as many as 1190 fledged young, whereas colony 1, which consisted of approximately 2130 breeding pairs, only produced approximately 460 fledged young. Data is partly obtained from Larsson and Forslund (1994).

colonies on Gotland and Öland is shown in Fig. 4. The total production of fledged young as well as the mean number of fledged young per breeding pair varied considerably among years and colonies. For example, in colony 1 the total yearly production of fledged young was relatively constant between 1983 and 1997 despite the number of breeding pairs during the same time period showing an almost 10-fold increase, from about

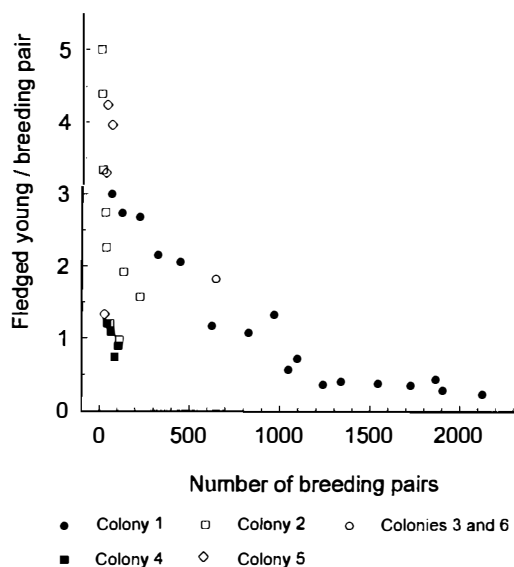


Fig. 5. Mean number of fledged young per breeding pair in relation to number of breeding pairs in six barnacle goose colonies on Gotland and Öland.

225 to about 2,130 breeding pairs (Fig. 4). The number of fledged young per breeding pair in the small colonies varied greatly, but on average the numbers were comparable to those observed in colony 1 during its early growth phase. When the available data for all six colonies were pooled, a negative relationship was found between the number of fledged young per breeding pair and number of breeding pairs (Fig. 5). For example, the mean number of fledged young per breeding pair was 2.7 (SD = 1.4, N = 14 years), 1.7 (SD = 0.6, N = 12 years), and 0.4 (SD = 0.2, N = 9 years) in years when colonies consisted of less than 100, between 100 and 1,000 and more than 1,000 breeding pairs, respectively (Fig. 5). As a consequence of the strong density-dependent effects on reproduction in the largest colony, most of the young which were produced on Gotland in 1997 actually originated from the smaller colonies (Fig. 4).

The limited information available on the production of fledged young in the colonies in Estonia and Finland indicate that some of the smallest colonies have been very productive (Laine 1996; Leito 1996). For example, during the first six years after the establishment of the oldest Estonian colony, the mean production of young in was about 4.2 fledged young per breeding pair (Paakspuu & Mägi 1986; Leito 1996). The

only available information on the production of young in the colonies in the city of Stockholm is from 1994 when about 0.85 fledged young were produced per breeding pair (Lindborg 1997).

Total number of individuals

To estimate the total number of individuals in the Baltic population, we used the following equation:

$$\text{Ind97} = (2 \cdot N97) + (Y97) + (Y96 \cdot S1) + (Y95 \cdot S1 \cdot S2 \cdot P2) + (Y94 \cdot S1 \cdot S2 \cdot S2 \cdot P3),$$

where Ind97 is the total number of individuals in Sweden, Estonia and Finland at the end of July in 1997, N97 is the estimated number of nests (breeding pairs) in 1997, Y94, Y95, Y96 and Y97 are the estimated total number of fledged young in 1994, 1995, 1996 and 1997, respectively, S1 is the estimated survival rate from fledging to subsequent summer, S2 is the estimated yearly survival rate from second summer and onwards, P2 is the proportion of two-year olds that do not breed, and P3 is the proportion of three-year olds that do not breed. Thus, the five terms within brackets to the right represent number of breeders, fledged young, one-year olds, two-year olds that do not breed, and three-year olds that do not breed, respectively.

Direct counts of the number of fledged young were not performed at all breeding sites in 1994 and onwards. When direct counts were lacking, we assumed that colonies of less than 100 pairs produced 2.7 fledged young per breeding pair, and colonies between 100 and 1000 pairs produced 1.7 fledged young per breeding pair (see above). No counts of the number of breeding pairs in Stockholm were performed in 1996. That number was estimated by calculating the mean of the number of breeding pairs observed in 1995 and 1997. The number of breeding pairs elsewhere in Sweden, i.e. outside Gotland, Öland and Stockholm, in 1997 was assumed to be equal to the number observed in 1996 (Fig. 3). Furthermore, we assumed that the mean survival rate of fledged young up to the subsequent summer was 86% (van der Jeugd & Larsson 1998), and the yearly mean survival rate of older birds was 94% (Larsson et al. 1998). We also assumed that the proportion of birds that did not breed at two and three years of age on average was 70% and 30%, respectively. Hence, all birds

of four or more years of age were assumed to breed.

Under these assumptions, the estimated total population size at the end of July in the year of 1997 can be estimated to be approximately 17,000 individuals $((2 \times 3,990) + (3,650) + (3,420 \times 0.86) + (2,970 \times 0.86 \times 0.94 \times 0.70) + (2,230 \times 0.86 \times 0.94 \times 0.94 \times 0.30) = 16,760)$.

Discussion

The data presented in this paper clearly show that the barnacle goose, a species which 30 years ago was exclusively found breeding in the High Arctic, is able to survive and successfully reproduce also in a variety of temperate environments (Figs. 2 and 3). Our estimate of the total size of the Baltic population leaves room for some uncertainties. For example, the production of fledged young might have been overestimated in those colonies where the number of fledged young were not directly counted; this may to some extent have inflated the final estimate. On the other hand, it is possible that the input values chosen for the proportion of the two- three-year olds that do not breed were somewhat low, and that a small fraction of the four or more year old birds do not make breeding attempts in all years, causing the final estimate to be too low. Furthermore, the final estimate is also dependent on the assumption that there is no net emi- or immigration to or from the Arctic Russian population. Although there are uncertainties connected with the size estimate, we find it likely that the Baltic barnacle goose population at the end of July in 1997 consisted of about 17,000 individuals. If this is the case, the number of individuals in the Baltic population has increased by about 40% per year since 1971, the year when the first natural breeding attempt was recorded in the Baltic region. To our knowledge, no other wild goose population has been recorded to have as high a rate of increase as this population.

The available data on fledgling production not only show that the number of fledged young per breeding pair decreased when the number of breeding pairs in colonies increased, but also that there seemed to be consistent differences in fledgling production among different colonies (Figs. 4 and 5). As a consequence, colony 1 in 1997 hosted more than 50% of the total number of

Baltic breeding pairs but produced less than 15% of the total number of fledged young. This shows the need to consider different colonies as separate, but interacting, demographic units when studying regulation processes in populations of colonially breeding geese or other colonially breeding birds.

Although we have found evidence for strong density-dependent effects on the survival of young before fledging (Fig. 4) (Larsson & Forslund 1994), we find it likely that the Baltic population will continue to increase in coming years, with the most rapid increase in breeding pairs occurring in medium sized colonies. We also expect new colonies to be established. Previous studies have shown that the main proximate cause for gosling mortality before fledging is predation by herring gull *Larus argentatus*, greater black-backed gull *Larus marinus*, lesser black-backed gull *Larus fuscus* (Forslund 1993), and at certain sites to some extent also by white-tailed eagle *Haliaeetus albicilla*, golden eagle *Aquila chrysaetos* and red fox. In 1997, for example, about 7,000 hatched young from colony 1 (more than 90% of all the hatched young) disappeared before fledging mainly due to predation by gulls. In the future, we expect that the numbers of Baltic barnacle geese will eventually be limited, not by the availability of nesting grounds or feeding opportunities for adults and fledged young, but by the availability of predator-safe grazing grounds with short protein rich grass which are needed by families with newly hatched young.

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Correlates of predator abundance with snow and ice conditions and their role in determining timing of nesting and breeding success in Svalbard light-bellied brent geese *Branta bernicla hrota*

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Tusenøyane in southeast Svalbard is the main nesting area of the Svalbard population of light-bellied brent goose. Field studies in Tusenøyane in 1987, 1989 and 1991 show that nesting geese are subject to heavy nest predation pressure by polar bears *Ursus maritimus*, and in some years arctic foxes *Alopex lagopus* prevent geese from attempting to nest. Polar bears are most abundant when there is dense pack ice in the surrounding Barents Sea. Geese nesting in territories with high snow cover during early incubation suffer the heaviest predation pressure. Sea-ice cover in the Tusenøyane area, as shown by satellite imagery, at the time of incubation explained 58% of the variance in breeding output of the population as a whole ($n = 17$ years). Nest predation pressure appears to be a major factor in limiting the ability of the Svalbard population of light-bellied brent geese to recover to its former size.

Geese arrive at Tusenøyane during the first week of June, but wait 7–10 days before laying eggs. Eggs hatch at a time when the quality of the preferred food plant, *Cochlearia officinalis*, has started to deteriorate and when most of plants of highest quality and size have already been depleted by the adult birds. It is suggested that the timing of nesting is a compromise between optimal food quality and avoidance of nest predation by polar bears.

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Introduction

The Svalbard light-bellied brent goose population constitutes one of the smallest and most vulnerable goose populations in the world (Madsen et al. 1996). Early in the 20th century, the population probably numbered in excess of 50,000 individuals (Salomonsen 1958) but crashed during the 1930s and 1940s, probably due to a combination of factors operating on the breeding grounds and in the wintering quarters in Denmark and England (Madsen 1987). In the 1960s, the population numbered 2,000–3,000 individuals, but following protection in Denmark from 1972 onwards numbers have increased to 4,000–6,000 individuals during the 1990s (Clausen et al. 1998). Productivity, which has been systematically assessed since 1980 by the proportion of juveniles in the autumn and winter flocks in Denmark and

northeast England, is generally low but variable (Madsen 1984; Clausen et al. 1998). Studies on the main breeding grounds, Tusenøyane in southeast Svalbard, have shown that breeding success is strongly influenced by predation mainly by polar bears *Ursus maritimus* and, at least in some years, by arctic foxes *Alopex lagopus* (Madsen et al. 1989, 1992).

This paper examines the effects of climatic conditions, predation and food supply and quality on the breeding success of the light-bellied brent geese and discusses the relative influence each component has on the timing of nesting. The material presented is based on three seasons of field work in Tusenøyane and 18 years of winter population counts and assessment of productivity, which provide the basis for an analysis of the influence of environmental factors on the breeding grounds affecting breeding output.

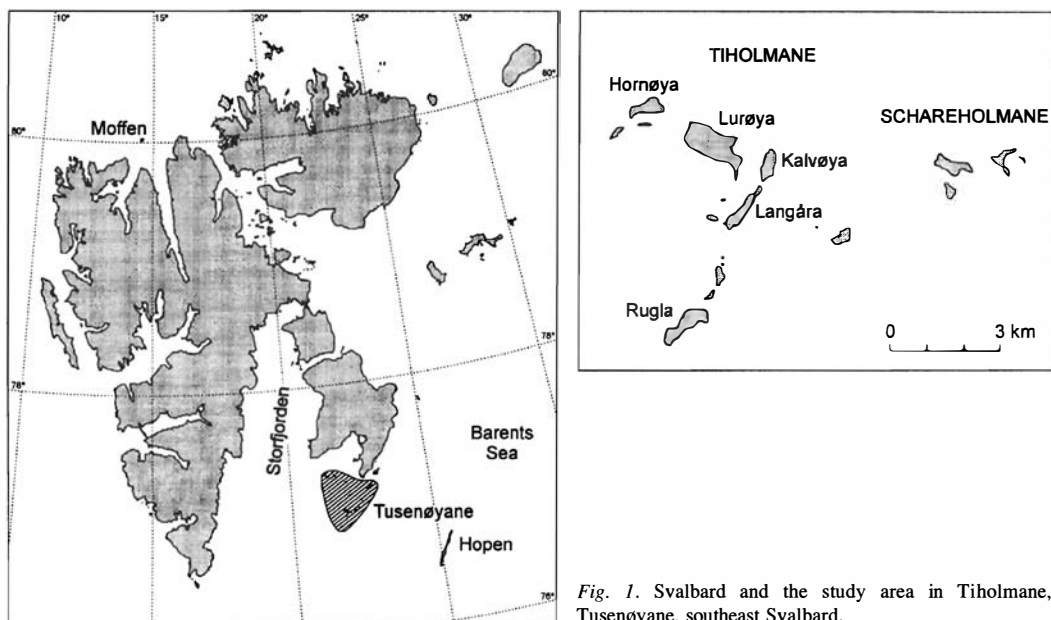


Fig. 1. Svalbard and the study area in Tiholmane, Tusenøyane, southeast Svalbard.

Study population

The Svalbard population of light-bellied brent geese breeds on islets around Svalbard, with the main known concentrations in Tusenøyane. In the northern fjords of Spitsbergen (Wijdefjorden, Woodfjorden) and Moffen, breeding pairs have been observed as well, with numbers of nesting pairs on Moffen varying between 2–3 and 43 (Norwegian Polar Institute unpubl.). In other areas of Svalbard, only a few nests or broods have been recorded. In Franz Josef Land, some breeding records have been documented, but no overall estimate of numbers exists (Clausen *et al.* 1999). Recently, satellite tracking of individuals caught in the Danish spring staging areas has demonstrated that the light-bellied brent geese breeding in northeast Greenland, primarily in Kilen (Hjort *et al.* 1987; Hjort 1995) belong to the same population as the Svalbard geese (Clausen & Bustnes, this volume). Approximately 850 birds were recorded in Kilen during the summer of 1985, including approximately 100 family groups (Hjort *et al.* 1987).

In Tusenøyane, three surveys of breeding pair numbers have been made. In 1985, Persen (1986) estimated the population at between 435 and 600 breeding pairs; in 1989, Madsen *et al.* (1992)

recorded 11 pairs, and in 1995, Bustnes *et al.* (1995) recorded 67 pairs. Based on the winter census data, it is calculated that in those three seasons the number of successful breeding pairs in the population as a whole was 476–600, 49 and 77–97, respectively (Clausen *et al.* 1999). The available information suggests that the majority of successful pairs reproduce in Tusenøyane and that conditions there largely determine breeding success in the population as a whole. Apparently, the northeast Greenland segment does not contribute many successful breeding pairs in all seasons.

Study area

The Tusenøyane archipelago (Fig. 1) consists of low and rocky islets with varying degree of vegetation cover and polar desert-like plant communities. Lurøya in the Tiholmane island group is outstanding with many ponds and a high degree of vegetation cover. This is also the island with the highest number of nesting brent geese (Madsen *et al.* 1989). Two vegetation zones are identified: (1) a wet moss carpet with protruding *Cochlearia officinalis*, and more patchily, *Saxifraga hyperborea*; and (2) a fjellmark dominated

by mosses and lichens with varying densities of *Saxifraga caespitosa*, *S. oppositifolia* and *Cochlearia*. *Cochlearia* and mosses constitute the most important food plants of geese throughout incubation and post-hatching (Madsen et al. 1989).

Potential predators of brent geese are glaucous gull *Larus hyperboreus*, arctic skua *Stercorarius parasiticus*, great skua *Stercorarius skua*, arctic fox and polar bear. Gulls and skuas nest on the islands. Arctic foxes were abundant on most islets in 1989; in 1985, 1987 and 1991, no foxes were observed (Persen 1986; Madsen et al. 1989, Madsen unpubl.). In 1992, foxes were recorded on Lurøya/Kalvøya (I. Gjertz, Norwegian Polar Institute, pers. comm.), but in 1993 and 1995, foxes were not seen (I. Gjertz pers. comm.; Bustnes et al. 1995). Storfjorden/Tusenøyane is the main early summer concentration area for polar bears in Svalbard (Wiig 1995), and on Lurøya, polar bears were regularly present while there was pack ice in the surrounding Barents Sea (Madsen et al. 1989).

Material and methods

Itinerary

Field work was carried out in 1987, 1989 and 1991. In 1987, Lurøya and adjacent islands in Tiholmane, Tusenøyane (Fig. 1) were visited from 13 June to 30 July (Madsen et al. 1989; Bregnballe & Madsen 1990); in 1989, most of the Tusenøyane islands were surveyed between 22 July and 4 August (Madsen et al. 1992); in 1991, Lurøya was visited during the period 4 June–7 July (Madsen unpubl.).

Field observations

On Lurøya in 1987 and 1991, efforts were made to identify all nesting pairs and the fate of their nests. To minimise disturbance, all records were made from a hide constructed on the top of the islet, supplemented by observations from other observation points. In 1987, the hide was placed at ground level, but in 1991, it was set on 3 m high

legs. In the middle of the nesting period, all known nests were visited once to record clutch sizes. Just after hatching in 1987 and just prior to hatching in 1991, nests were revisited to record the fate of the eggs. Egg-laying dates were extrapolated from known hatching dates and clutch sizes or from the date of start of incubation (Madsen et al. 1989). Activity budgets of nesting pairs were systematically recorded for long periods throughout the incubation period, and in this manner, predation attempts/success, nest attendance and nest desertions were monitored.

Snow cover on Lurøya was monitored daily by visual estimation of the coverage throughout the central plain and in individual goose territories. Pack-ice cover in the surrounding Barents Sea was estimated on a daily basis. In 1987, daily maximum and minimum temperatures were recorded.

Densities and exploitation rates of *Cochlearia* were measured after incubation in 1987 (Madsen et al. 1989) and throughout incubation in 1991. In 1991, 625 cm² plots were put out in wet moss carpets in two goose territories at the time of snow melt. In one of the territories four plots were established, in the other three plots. Every fourth day from 19 June to 7 July, plots were revisited. A frame with a grid was superimposed and each *Cochlearia* rosette was plotted on a grid map with a note on the proportion of the rosette removed by the geese.

To estimate growth rates of *Cochlearia*, individual ungrazed plants were randomly collected from a wet moss carpet close to the camp site at weekly intervals from 27 June (snow melt) to 29 July 1987. Plants were sorted into first and second year plants, and into roots and above-ground material. Dead material was separated from the above-ground material. In the field, the plant material was dried over a stove; in the laboratory, the material was oven dried and individually weighed. As a crude measure of food quality, pooled samples were analysed for nitrogen content (Kjeldahl technique) by the National Agricultural Science Laboratory. Each sample was analysed in duplicate.

Weather and ice conditions

In order to relate ice conditions (as a proximate indicator of polar bear abundance; see below) to

breeding success of the population as a whole, satellite imageries of ice densities for the Barents Sea region were analysed for the years 1980–1997. Imageries available from approximately 20 June, i.e., early in the incubation period, were used. Based on the maps, the ice density in the Tusenøyane/Storfjorden area was classified by percentage cover (by steps of 10%). A 50 km × 50 km grid covering Tusenøyane and the adjacent 50 km (n = 9) was superimposed on the satellite imagery; ice coverage was computed as the mean of the coverage in the nine cells.

To relate weather conditions and snow melt to timing of nesting and overall breeding success, daily mean temperatures and snow coverage were obtained from Hopen meteorological station, positioned 90 km southeast of Tiholmane. Snow coverage estimates were unfortunately stopped at Hopen in 1983. As an alternative predictor of the timing of snow melt, the date after 1 June when the cumulative positive daily mean temperature reached 6°C was used. This estimate was derived from the meteorological data from Hopen, where the temperature sum was on average 5.8°C (± 1.1 95% c.l.; n = 9) on the date when snow coverage decreased from 75% to 50%.

Maximum and minimum temperatures recorded during June and July 1987 at Lurøya and Hopen, respectively, corresponded grossly with no systematic difference. Weather data from Hopen are therefore assumed largely to reflect the situation in Tusenøyane.

Results

Timing of nesting

In 1987, median date of start of incubation was 15 June (range 11–25 June) and median hatching date was 7 July (range 4–18 July). In 1991, the first brent geese had arrived to Lurøya before 4 June; the majority of birds arrived during 5–7 June. Copulations were observed during 7–12 June. Median date of start of incubation was 16 June (range 12–20 June) (Fig. 2).

In both years, egg laying and incubation were initiated at the time of start of snow melt (defined as decreasing snow cover) (Fig. 2). In 1987, snow melt progressed faster than in 1991, but in 1987 a

snow blizzard in the first days of July caused a partial snow coverage of the island.

In relation to the general climatic conditions recorded at Hopen, the geese arrive while daily mean temperatures are still below 0°C, but from mid June to mid September, daily mean temperatures are above the freezing point (Fig. 3). At Hopen, time of snow melt varied between 13 June and 7 July (mean date when the cumulative positive daily mean temperature reached 6°C was 21 June ± 3 (95% c.l.; n = 18)), and the time of snow melt at Lurøya in 1987 and 1991 occurred within the first half of that range. At Hopen, the date of first complete snow cover fluctuated between early September and mid October, with a mean of 28 September (± 12; n = 9).

Predator abundance

In 1987, 10 pairs of glaucous gulls and 4 pairs of arctic skuas nested on Lurøya, and in 1991, 12 pairs and 5 pairs, respectively. In addition, in 1991, a pair of great skuas defended a territory. Non-breeding pomarine skuas *Stercorarius pomarinus*, long-tailed skuas *S. longicaudus* and great skuas were seen irregularly.

Polar bears were regular on the island while there was pack ice. In 1987, bears were observed on the island on average every other day between 14 June and 12 July. After the disappearance of pack ice, no bears were recorded (Fig. 4). In 1991, polar bears were more abundant, with up to five individuals per day in the first half of June when the pack ice was most dense.

In 1987 and 1991, arctic foxes were absent. However, in 1989, arctic foxes were present on most islands in Tusenøyane, including Lurøya (Madsen *et al.* 1992).

Nesting success

In 1987, it was estimated that a total of 38 nests were initiated on Lurøya; in 1991, 47 nests (Table 1). In both years, few nests were subject to predation due to disturbance by the observers. In both years (most profoundly in 1991), the major cause of nest loss was egg predation by polar bears. It was mainly female polar bears (with and without cubs) which specialised in searching for

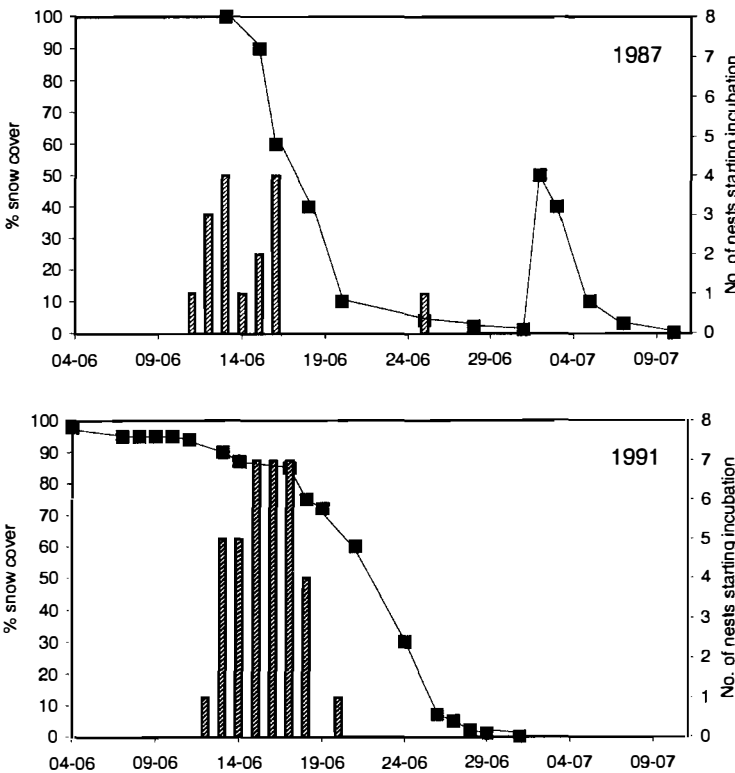


Fig. 2. Start of egg-laying (bars) by light-bellied brent geese on Lurøya, 1987 and 1991 in relation to snow cover in the central plain of Lurøya (curve).

nests of geese, eiders *Somateria mollissima*, gulls and skuas (Fig. 5; Madsen et al. unpubl.). In most situations, geese flushed 5–10 m in front of the polar bear, and the polar bear then located the nest. In some situations, female brent geese left

their nests at a long distance from the approaching bear, without covering their eggs with down. These nests were not found by the bears, but lack of nest defence gave access to egg predation by arctic skuas (and more infrequently by glaucous

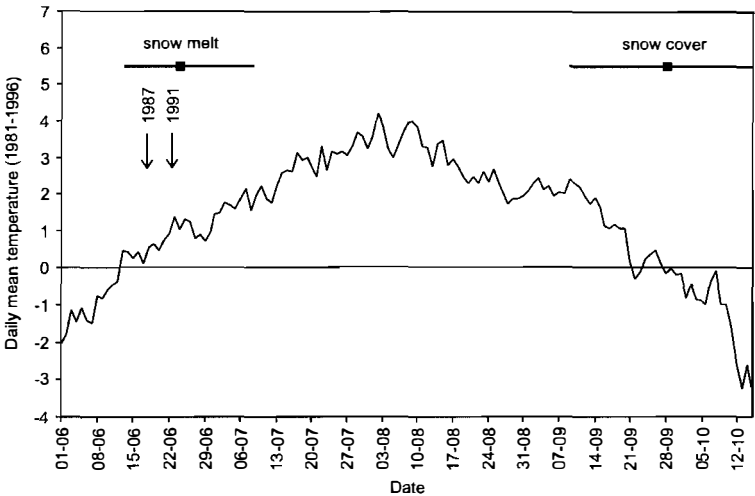


Fig. 3. Daily mean temperatures (average of 1981–1996) at Hopen meteorological station and the period of snow melt and late summer snow fall (snow data from 1970–1983). Averages of first day of snow melt (snow coverage decreasing from >75% to 50%) and first day of snow coverage (>75%) are shown by filled squares, and horizontal bars show the range. The observed dates of snow melt on Lurøya in 1987 and 1991 are shown by arrows. Source: Norwegian Meteorological Institute.

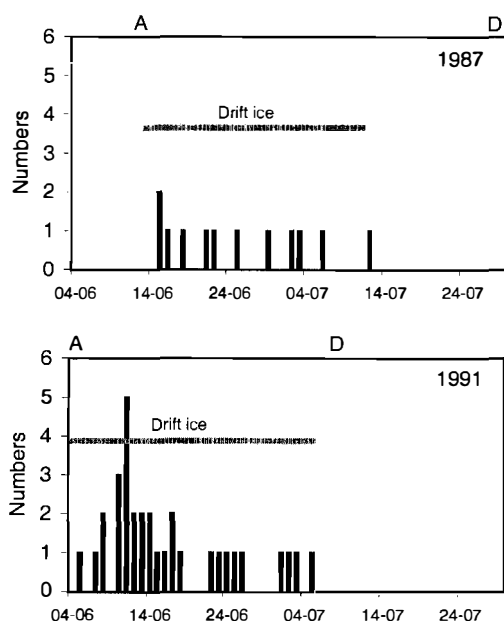


Fig. 4. Daily number of observed adult and immature polar bears on Lurøya in 1987 and 1991. Horizontal bars show the period of pack ice in the surrounding Barents Sea. A denotes start of observation and D end of observation.

gulls) which were constantly patrolling the nesting area while trespassed by a polar bear.

Skuas and glaucous gulls by themselves were not severe egg predators in undisturbed situations and they mainly caused partial nest predation. Successful egg predation only took place during nest recesses taken by the females, whereas during

female nest attendance, ganders were always successful in chasing away avian predators.

In both 1987 and 1991, some nests were deserted by females during the last stage of incubation. Excluding the clutches lost due to observer disturbance, 26% and 13% of the eggs produced hatched.

Egg predation by polar bears was most severe during the first half of the incubation period, when snow cover was still extensive. At that time, the bears walked from one snow-free patch to another searching for nests. In both years, in territories where nests were subject to predation by bears, snow cover at the start of incubation was higher compared to territories which were not subject to predation (Fig. 6). However, in 1991 after snow melt, a female polar bear appeared which was actively searching for bird nests. Within less than 24 hours, the bear emptied four goose nests and many nests of eiders and gulls.

In both years all deserted nests (Table 1) were from territories with less than 50% snow cover at the start of incubation.

Supplies and quality of *Cochlearia*

In 1987 it was found that almost the entire above-ground biomass of *Cochlearia* in the wet moss carpet had been removed by the geese during incubation, whereas in the dry moss carpet and fjellmark, the geese had only exploited the plants to a limited extent (Madsen *et al.* 1989). In plants

Table 1. Nesting success of light-bellied brent geese, Lurøya, Tusenøyane, Svalbard 1987 and 1991.

	1987		1991	
	Nests	Eggs	Nests	Eggs
Start of egg-laying	38	152	47	188
Disturbed by observers	3	12	1	4
Predated by polar bears	12	48	31	87
Disturbed by polar bears, predated by skuas/gulls	9	37	2	10
Predated by skuas	0	2	1	6
Predated by gulls	0	0	0	2
Deserted	4	11	5	12
Hatching failure	0	6	0	0
% hatching ¹	28.6	25.7	17.0	12.8

¹excluding disturbance by observers.

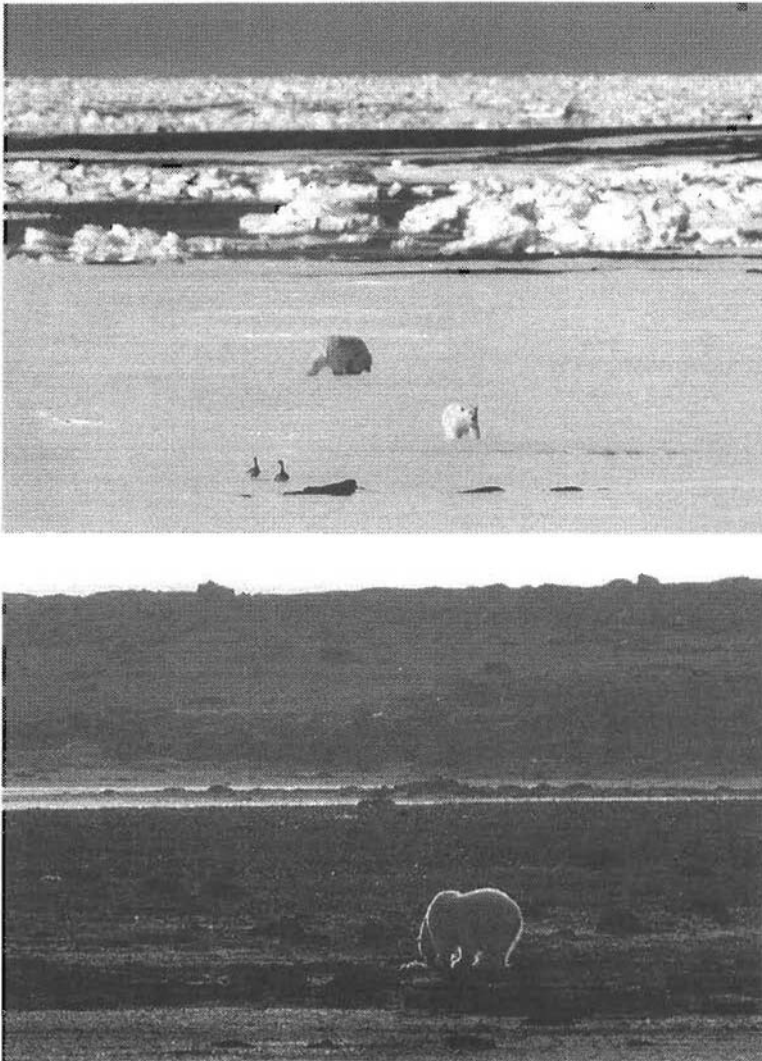


Fig. 5. Polar bears plundering goose nests on Lurøya, June 1991. Upper photo: a female bear and a cub. Photo below: a female bear. Down from six previously plundered goose nests can be seen. Photos: John Frikke.

randomly collected in wet and dry moss carpets on 3 July 1987, it was found that the fjellmark plants were smaller than plants in the wet moss carpet, i.e. in first-year plants 3.7 mg above-ground biomass per plant versus 8.4 mg ($n = 35$ for each; $t = 2.57$, $P < 0.01$), and in second-year plants 10.2 mg versus 31.0 mg ($n = 35$ for each; $t = 2.07$, $P < 0.05$). Furthermore, the protein content in the above-ground biomass was lower in the fjellmark plants compared to the wet moss carpet plants, i.e. in first-year plants 23% versus 32% and in second-year plants 21% versus 29% (one sample per category).

In 1991, the exploitation of *Cochlearia* in wet

moss carpets was followed from snow melt until hatching in a territory occupied by a nesting pair and in a territory abandoned following nest predation on 22 June. After nest predation the latter territory was used by the pair for 2–3 days and later by neighbouring nesting pairs and on some days by non-breeding pairs. In the occupied territory, the above-ground biomass of *Cochlearia* was completely depleted in two plots and reduced by more than 50% in the third. In the abandoned territory, the biomass at hatching in four plots was reduced to 10–40% of the biomass at the time of snow melt (Fig. 7).

In a wet moss carpet not exploited by geese

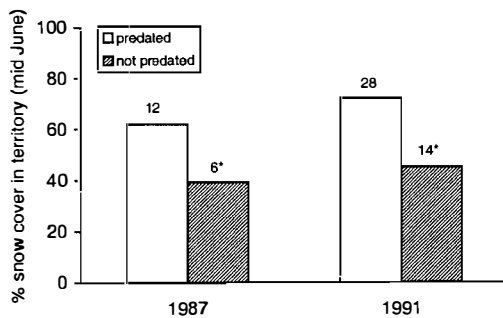


Fig. 6. Snow cover at the start of incubation in territories of light-bellied brent geese which were subject to predation and not subject to predation in 1987 and 1991, respectively. Labels show sample size, and asterisks indicate that the difference in snow cover of predated and not predated territories was significant (χ^2 -test, $P < 0.05$).

(close to camp site), the average above-ground biomass of individual first-year and second-year *Cochlearia* plants doubled from the time of snow melt to the end of July 1987, whereas average root biomass was unchanged (Fig. 8). However, due to high variation around the means the increase in above-ground biomass was not statistically significant (ANOVA). The biomass of dead above-ground material was unchanged during the period. The protein content of the *Cochlearia* above-ground plant parts as well as roots was highest just after snow melt and gradually decreased thereafter (Fig. 9).

Relationship between condition factors and breeding success

The following factors were used in a regression model exploring the effect of conditions operating on Tusenøyane on overall breeding success:

(1) The ice situation in the Tusenøyane area around 15–20 June. The ice situation varied considerably between years (Fig. 10). Because polar bears primarily follow the pack ice which retreats from the southwest towards the northeast, the percentage ice cover (arcsine transformed) is used as a proximate predictor of polar bear abundance. Arcsine transformed data were normally distributed (Shapiro-Wilk test for normality, $P < 0.001$).

(2) Date of snow melt. As the polar bear predation pressure was shown to depend on snow

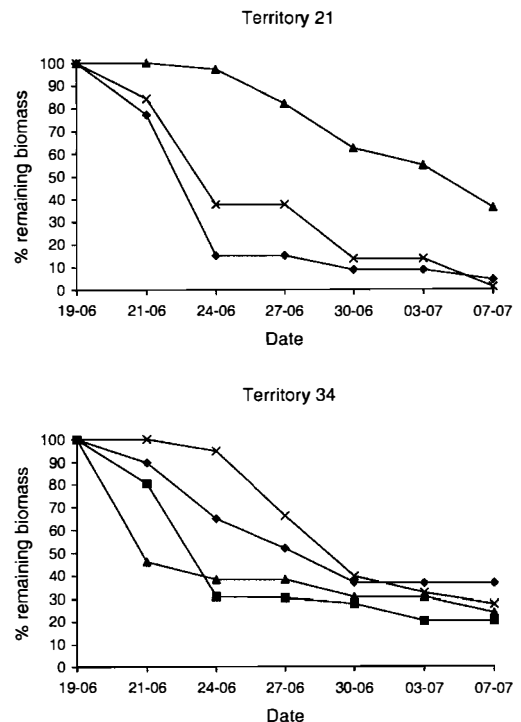


Fig. 7. Rate of exploitation of *Cochlearia officinalis* in plots (each plot shown by a symbol) in wet moss carpets in two territories of light-bellied brent geese (Lurøya 1991). Territory 21 was occupied until hatching (early July), whereas territory 34 was abandoned after predation on 22 June. Snow melt took place during 19–24 June.

coverage in the territories, the time of snow melt is likely to influence nest success. Furthermore, in late years, females may encounter poor feeding conditions leading to increased nest desertion. The day number after 1 June when the positive mean temperature sum reached 6°C was used as a predictor (see Material and methods). Data were normally distributed (Shapiro-Wilk test for normality, $P < 0.001$). Ice cover around 15–20 June and date of snow melt were not correlated ($r = -0.160$, $P > 0.05$).

(3) Presence of arctic fox. It is assumed that the presence of one fox on an island at the time of egg laying will cause a complete abandonment of nesting (Madsen *et al.* 1992). In three years out of seven years with surveys of at least Tiholmane, arctic foxes were present, i.e. in 1989, 1992 and 1993, but not in 1985, 1987, 1991 and 1995. The 1989 and 1992 fox years coincide with years with high abundance of arctic foxes in Taimyr, north

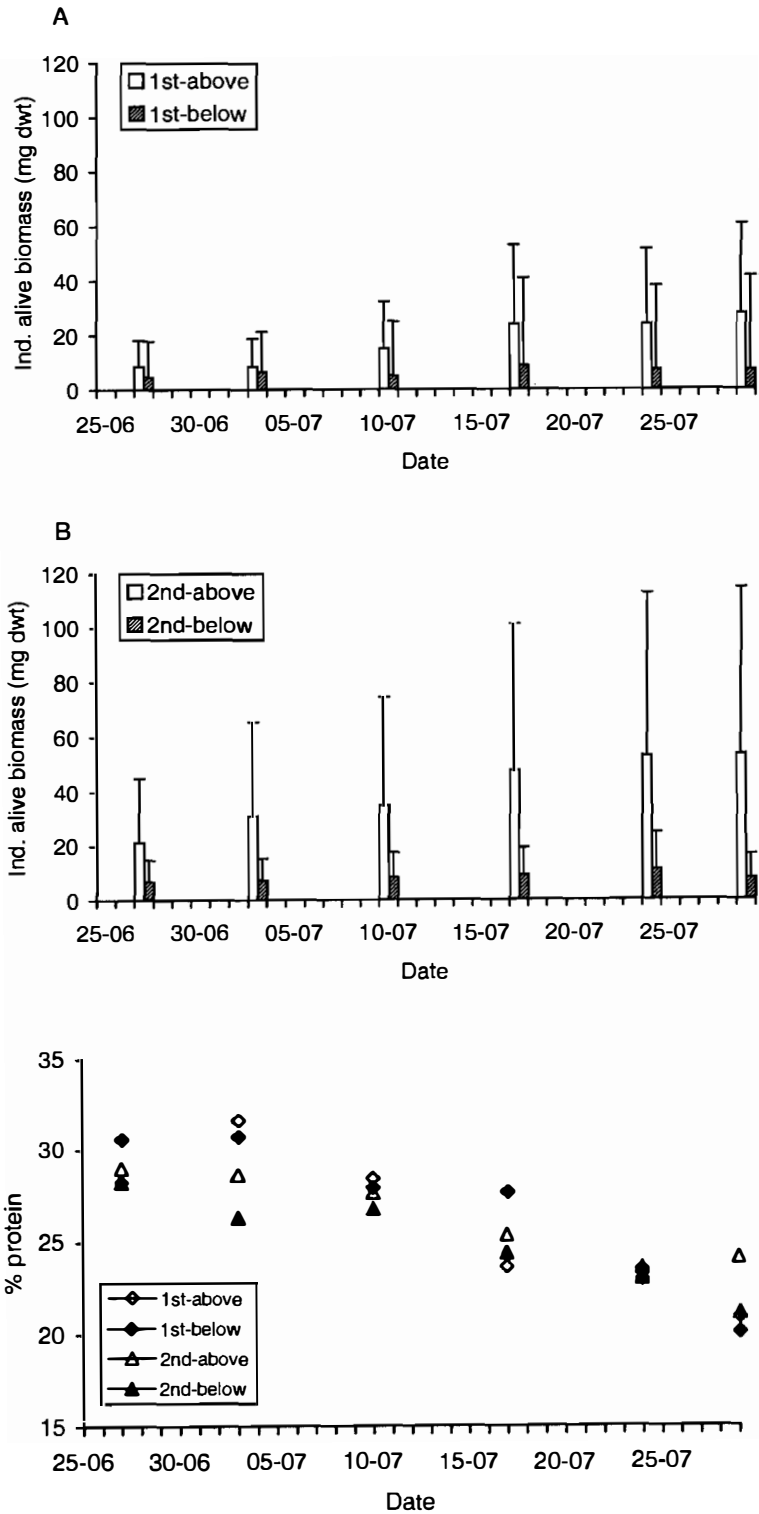


Fig. 8. Growth in biomass of above-ground alive tissues and roots of *Cochlearia*, divided into first-year plants (A) and second-year plants (B). Each sample consists of 35 ungrazed plants or more, collected at random in a wet moss carpet on Lurøya in 1987. Bars show 95% confidence limits.

Fig. 9. Protein content of above-ground live tissues and roots of *Cochlearia* from late June to late July (Lurøya 1987), divided into first-year plants and second-year plants. The decline is significant in all four categories (Pearson correlation, $P < 0.01$).

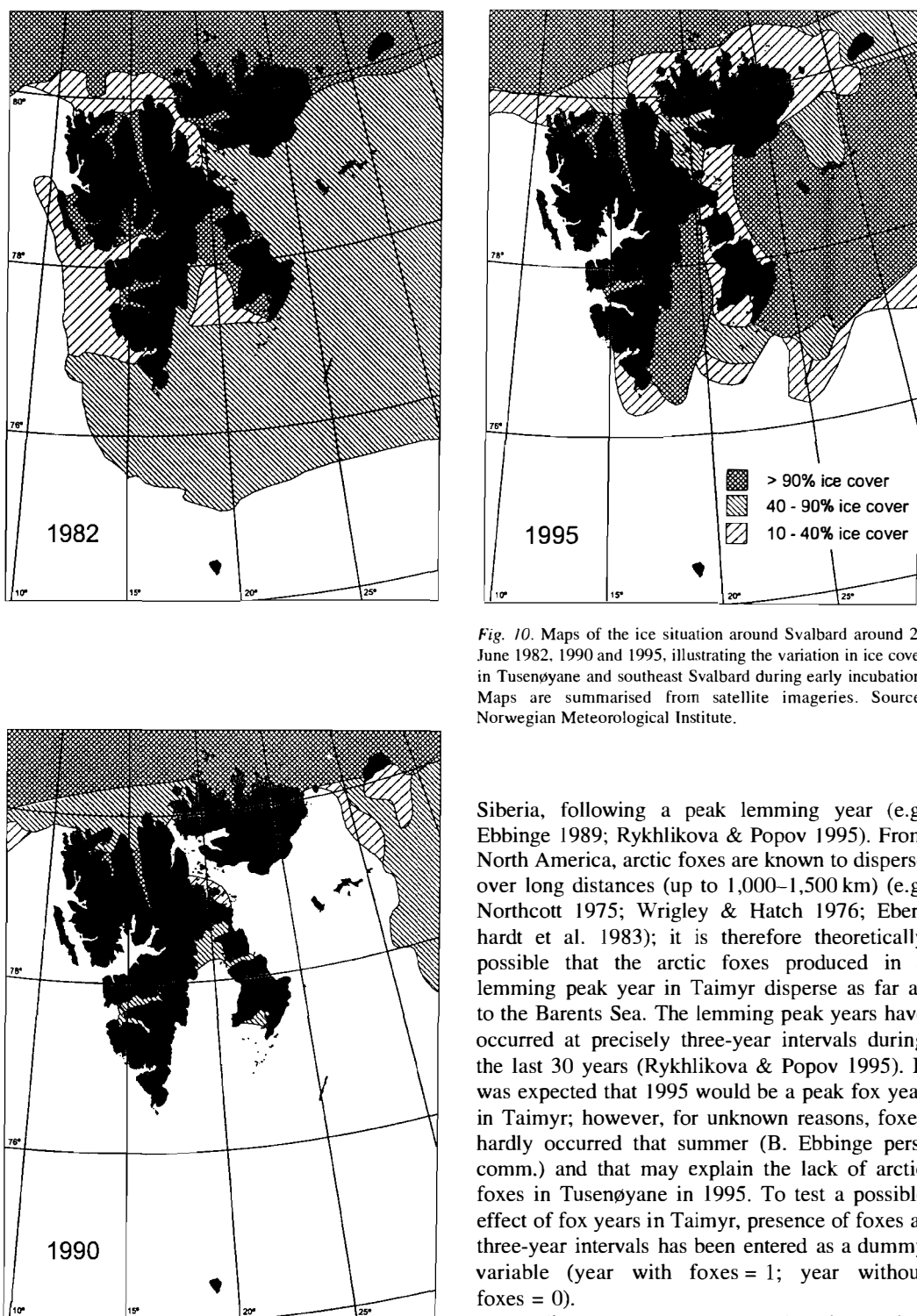


Fig. 10. Maps of the ice situation around Svalbard around 20 June 1982, 1990 and 1995, illustrating the variation in ice cover in Tusenøyane and southeast Svalbard during early incubation. Maps are summarised from satellite imageries. Source: Norwegian Meteorological Institute.

Siberia, following a peak lemming year (e.g. Ebbinge 1989; Rykhlikova & Popov 1995). From North America, arctic foxes are known to disperse over long distances (up to 1,000–1,500 km) (e.g. Northcott 1975; Wrigley & Hatch 1976; Eberhardt *et al.* 1983); it is therefore theoretically possible that the arctic foxes produced in a lemming peak year in Taimyr disperse as far as to the Barents Sea. The lemming peak years have occurred at precisely three-year intervals during the last 30 years (Rykhlikova & Popov 1995). It was expected that 1995 would be a peak fox year in Taimyr; however, for unknown reasons, foxes hardly occurred that summer (B. Ebbinge pers. comm.) and that may explain the lack of arctic foxes in Tusenøyane in 1995. To test a possible effect of fox years in Taimyr, presence of foxes at three-year intervals has been entered as a dummy variable (year with foxes = 1; year without foxes = 0).

Breeding success was expressed as the number

Table 2. Output of multiple linear regression analysis of the relationship between breeding success of light-bellied brent geese as assessed on the wintering grounds (PROD), date of snow melt (S), presence of arctic fox (A) and ice coverage (C). The time series is 1981–1997 ($n = 17$). See text for explanation of variables. As indicated by the superscripts in the regression equation, snow melt and fox presence did not contribute significantly to the model, and were excluded in the parsimonious model using only ice cover as variable.

Model variables	Regression equation	R ² (%)	F
S, A, C	$PROD = 0.844^{**} + 0.005S^{ns} - 0.046A^{ns} - 0.585C^{**}$	60.2	6.56 ^{**}
C	$PROD = 0.974^{***} - 0.627C^{***}$	57.9	20.60 ^{***}

Significance levels: ns: $P > 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

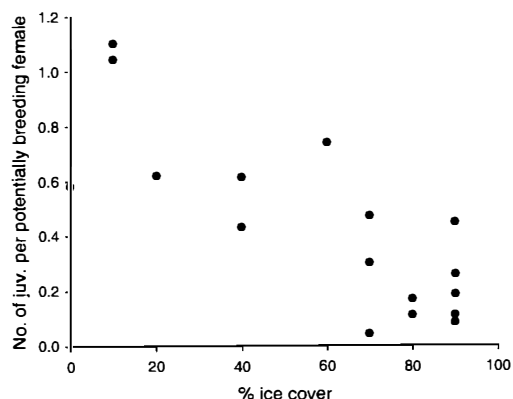


Fig. 11. Relationship between ice cover in Tusenøyane around 20 June and the breeding success in the population of light-bellied brent geese as a whole expressed by the number of offspring produced per potentially breeding female (data from winter surveys; NERI unpubl.).

of juveniles produced per potentially breeding female in the population as a whole. The number of potentially breeding females has been calculated on the basis of winter population data and age-ratio counts (P. Clausen pers. comm.).

The outcome of the multiple regression analysis is shown in Table 2. The model using all three variables explained 60% of the variance in breeding success, but date of snow melt and fox presence did not contribute significantly to the regression. Based on parsimonious model fit, the model using only ice cover as variable was highly significant and did not significantly reduce the explanatory power (58% of the variance explained) (Fig. 11).

Discussion

Timing of nesting

High Arctic breeding geese have a narrow time

window in which to complete reproduction and moult of flight feathers. Geese arrive early when most of the tundra is still snow covered. They rely heavily on endogeneous fat and protein stores built up during spring staging further south (in case of light-bellied brent geese in Denmark) for egg production and maintenance during pre-nesting and incubation (Ebbinge & Spaans 1995). There is much evidence to suggest that early arrival and nesting has evolved to synchronise hatching of goslings with the availability of food of the highest nutritional quality (Harwood 1977; Sedinger & Raveling 1986). Several studies on various arctic-nesting goose species have shown that there is a penalty for being late in terms of retarded gosling growth rate and consequent late summer body size, which has repercussions on first-winter survival (Owen & Black 1989; Cooch et al. 1991; Sedinger & Flint 1991; Prop & de Vries 1993; Schmutz 1993; Sedinger et al. 1995) and subsequent adult body size and fitness parameters (Sedinger et al. 1995; Choudhury et al. 1996; Loonen et al. 1997). However, arriving too early is also disadvantageous because of low temperatures, increased maintenance costs and reduced available food supply (Prop & de Vries 1993). This leaves the geese with a narrow optimal time-period for egg-laying; in Svalbard breeding barnacle geese less than two weeks (Prop & de Vries 1993).

In the High Arctic, the timing of nesting is also constrained by the autumn freeze-up and snow fall. In Tusenøyane, it appears that the light-bellied brent geese have time until approximately 10 September before heavy snow fall (Fig. 3). With egg-laying starting on 12 June, an egg-laying period of three days, 24 days of incubation (Madsen et al. 1989) and a fledging period of 40 days (Owen 1980), i.e. a total period of 67 days, goslings will fledge by 17 August by which time parents have also regained their powers of flight (Bregnballe & Madsen 1990). Thus, the geese do

not appear to be critically time-stressed during late summer due to climatic conditions.

The timing of egg-laying and hatching by light-bellied brent geese in Tusenøyane appears to be out of phase with the time when their preferred food plant, *Cochlearia*, is most nutritious. By the time of hatching, *Cochlearia* quality has started to deteriorate, and furthermore the nesting birds and non-breeders have depleted most of the resource of high quality, i.e. the *Cochlearia* in the wet moss carpet. Hence, this seems to be a case which does not support the 'food quality timing' hypothesis. The growth rate of *Cochlearia* is extremely low and cannot compensate for the exploitation by the geese. As the Tusenøyane islands are far from the main islands in eastern Svalbard, the geese are effectively locked in an area with limited food supplies of decreasing quality. Thus, rather than being time constrained, the goslings and parents are probably food constrained during post-hatching.

Why then, do the light-bellied brent geese not start nesting earlier? The light-bellied brent geese spend 6–10 days from arrival to egg-laying, and during this pre-nesting period the pairs establish territories, copulate and feed intensively on mosses and *Saxifraga* flower heads and leaves in the snow-free patches (Madsen & Frikke unpubl.); however, given the poor quality of the food, it is questionable that it is sufficient to maintain a balanced or positive energy budget. Theoretically, the light-bellied brent geese could start egg-laying almost immediately upon arrival, similar to the dark-bellied brent geese in Taimyr (Spaans *et al.* 1993); this would save important female energy reserves, and the timing of hatching would have been more optimal in relation to the later vegetation quality and abundance.

An important trade-off may be that by postponing egg-laying to mid June, snow melt will be in progress which reduces the risk of polar bear predation. As shown above, pairs with territories with high snow coverage suffer more from polar bear predation than pairs settling in territories with low snow coverage; however, pairs which establish territories on the snow-free patches (fjellmark) have poor feeding opportunities during incubation (e.g. *Cochlearia* of relatively low quality) and those females are at high risk of nest desertion before hatching because of poor body condition (indirectly witnessed by an extraordinarily increased time off the nest in the course of incubation; Madsen *et al.* 1989; Madsen & Frikke

unpubl.). Therefore, the use of the snow-free fjellmark is not a favourable alternative to the snow-covered marsh patches which gradually become free of snow during incubation.

The suggestion is that the timing of egg-laying in light-bellied brent geese is a compromise between two counteracting selective forces: optimisation in relation to vegetation quality pushing for early egg-laying and reduction of nest predation pushing for delayed egg-laying.

There exists no information on gosling growth rates; this is a high research priority in order to understand how the light-bellied brent geese cope under such harsh arctic desert conditions and how critical the timing of hatching is for gosling growth and first-year survival.

Impact of predators

Earlier, we suggested that the light-bellied brent geese were 'ecologically trapped' in Tusenøyane with little scope of expansion because (1) polar bears (and in some years arctic foxes) exert a heavy egg predation pressure and thereby affect population size, and (2) the competitively superior barnacle geese have now occupied the former breeding islets off the west coast of Spitsbergen (Madsen *et al.* 1989). Compared to Tusenøyane, the western coast is a 'haven' because of more abundant vegetation of higher quality and fewer polar bears. The recent discovery that the north-east Greenland light-bellied brent geese belong to the population and the observations of fair numbers of breeding pairs in northern Spitsbergen in some years is potentially relieving from a conservation point of view. However, the finding that 58% of the variance in breeding output in the population as a whole is explained by the ice conditions in Tusenøyane supports the hypothesis that this area remains central to the productivity of the entire population and that breeding success largely depends on predator abundance there. It is a research priority to learn more about the northeastern Greenland population segment and factors affecting its breeding performance, and likewise for the northern Spitsbergen breeders.

The insignificance of date of snow melt appears contradictory to the finding that polar bear predation was most severe in territories with high degree of snow cover. One explanation for the lack of relationship might be that there is too little

variation in the time of snow melt, especially a lack of years with early snow melt in relation to the time of egg-laying; another explanation might be that we have had to rely on an indirect measure of snow melt which was measured 90 km away from the central islets of Tusenøyane.

At present, it is not known which factors affect the presence of arctic foxes in the Tusenøyane islands. The suggestion that their occurrence may be influenced by the dispersal of foxes from northern Siberia cannot be substantiated further and was not supported by the regression analysis.

Only from 1987 does information exist about losses of goslings during their first three weeks after hatching. During these three weeks, average brood size and the number of broods in Tiholmane did not change ($n = 23$ broods) (Madsen et al. 1989). Information on rate of loss later during post-hatching does not exist.

Based on winter census data, age and brood counts, it has been calculated that annual mortality rate almost equals annual productivity (12.7% versus 14.5%; population mean 1981–1994) (Clausen et al. 1998). Nest predation pressure appears to be the main determinant of reproductive output, and is a major contributing factor limiting the ability of the Svalbard population of light-bellied brent geese to recover to its former size.

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Flyways of North Atlantic light-bellied brent geese *Branta bernicla hrota* reassessed by satellite telemetry

PREBEN CLAUSEN and JAN OVE BUSTNES



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The main goal of this study was to describe the migratory routes and identify stopover sites believed to be used by light-bellied brent geese on spring migration from their spring staging areas in Denmark to their breeding areas in Svalbard. Five birds were fitted with satellite transmitters in mid-May 1997 and four were tracked to their breeding or moult destinations. Two of the tracked birds migrated via pre-breeding staging areas in southern Svalbard, where they staged five to eight days, up to the northern parts of Svalbard to breed/moult. The two other birds, a pair, migrated along the western coast of Norway towards Svalbard, across the Greenland Sea to a pre-breeding staging area in Peary Land in northern Greenland, where they staged for two days before migrating southeast to breed/moult at Kilen, northern Greenland. One of the birds that migrated to Svalbard made a stopover in Vestfjorden near Lofoten, northern Norway, and the birds that migrated to Greenland made a stopover near Vega, western Norway. Judged from maps, these two sites would only have been used for roosting/drinking, but not feeding. Two of the transmitters were still operating after the moult. One bird remained in northeastern Svalbard at least until 8 September, when the transmitter terminated, and the other bird moved from Greenland via western Spitsbergen to Sørkappøya, the southernmost island in the Svalbard archipelago, where it staged at least until 8 September. No data was received from the bird between 9–22 September, but from 23 to 27 September it was staging in the northern part of the Danish Wadden Sea, and on 29 September it moved to the wintering site at Lindisfarne. The study leads to a reassessment of the flyways used by light-bellied brent geese in the North Atlantic. Traditionally the birds breeding in Greenland have been linked with those breeding in Arctic Canada, staging in Iceland and wintering in Ireland. This study shows that the present breeding population of light-bellied brent geese in northern Greenland is linked to the geese which breed in Svalbard and Franz Josef Land and winter in Denmark and England.

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Introduction

In a recent review of the population development, distribution and conservation status of the East Atlantic flyway population of light-bellied brent geese *Branta bernicla hrota*, Clausen et al. (1999) point out (1) that despite 40 years of fairly intensive study, gaps still remained in our knowledge of the migratory routes used by these geese between their wintering areas around the North Sea and the known breeding areas on Svalbard and Franz Josef Land, and (2) that the breeding and moulting distribution of the population was also only partly known. Especially puzzling was the time-lag between known departures from Denmark (peak 26–31 May) and arrivals to the

supposed main breeding area of Tusenøyane (southeast Svalbard) (peak 7–8 June). With an expected migratory speed of around 70 km/hour (Lindell 1977; 90 km/hour, corrected for wind assistance of 5–6 m/s tailwind = 18–21.6 km/hour), the geese should be able to make the approximately 2400 km journey in less than two days; judged from the field observations, the birds appeared to use seven to ten days. Clausen et al. (1999) concluded that stopover sites must exist somewhere en route between the spring staging areas in Denmark and the breeding sites in Svalbard, and that the importance of these sites, in terms of 'refuelling' sites, should be established.

Satellite telemetry has been used the past 10–15 years to track movements of mammals and birds,

and transmitters have recently been developed which are suitably small to use on medium-sized birds, such as the brent goose (e.g. Beekman et al. 1996; Lorentsen et al. 1998). Hence, the use of satellite telemetry seemed a suitable method for tracking brent geese when conduct a study aimed at identifying their suggested refuelling sites.

In this paper we present primary data on spring migration, pre-breeding, breeding and moulting as well as post-breeding distributions of the satellite tracked birds. We include ground-based data from Denmark, Lista (southwestern Norway), Svalbard and England to support the evidence obtained from the satellite telemetry study. In addition we give an overview of the performance of the satellite transmitters used – to update Benvenuti's (1993) overview of the current limitations of satellite telemetry for tracking geese. The study is a first step in a long-term study which has the ultimate goal of establishing the relative importance of the refuelling stops at the pre-breeding stopover areas to the breeding brent geese, and hence to the population development of the Svalbard light-bellied brent goose population. In a second paper we will address the flight energetics of the brent geese successfully tracked to the breeding areas.

Materials and methods

Seventeen light-bellied brent geese were caught on 15 May 1997 at Agerø, Denmark (56°43'N 8°33'E), which has been recognised as the most important spring staging area of the population since the mid 1980s (Clausen et al. 1998). All birds were ringed with individually recognisable combinations of engraved colour rings, which were legible at distances up to 300–400 metres under good conditions (Clausen & Percival 1992). Five of the birds were equipped with satellite transmitters. The intention was to apply the transmitters to males to avoid potential negative influence of transmitter attachments on the breeding performance of females (cf. Ward & Flint 1995). However, because we encountered problems with proper sexing, five individuals among the largest birds were chosen, based on biometrics, i.e. measurements of tarsus, wings, skull and weight. Subsequent behavioural observations in the field revealed that at least one of the birds was an adult

female, three were adult males, and the remaining one, an immature bird, was probably male.

Each bird was equipped with a 22 g Microwave Telemetry Inc. PTT (platform transmitter terminal) specially manufactured by Microwave. The transmitters were supplied with standard 20 g PTT, with the stronger, but heavier, antenna construction from their standard 30 g PTT. The PTT was glued with Loctite Superattak glue to the backs of the birds just behind their shoulders. The feathers at the attachment site (area 48 mm × 17 mm) were clipped halfway down to their base before gluing, so that after attachment the PTT would be partly covered by the surrounding feathers. In addition, the PTTs were fastened to the birds with a knickers elastics harness (2 g), following guidelines given by Glahder et al. (1998). Before the five birds were released with the transmitters, their vents and abdomens were dyed yellow with picric acid in alcohol solvent to ease subsequent identification in the field. Each PTT is recognised by an individual ID or bird identification code: 11599, 11600, 11601, 11602 and 11604. These codes are used throughout this paper.

Each PTT was supplied with a Multi-season Nano Timer, programmed to operate transmission according to the following protocol: 8 hours ON–15 hours OFF: 15 May–15 June 1997; 8 hours ON–170 hours OFF: 16 June–15 August 1997; and 8 hours ON–28 hours OFF: 16 August–until battery exhaustion. With an expected lifetime of 3½ weeks or 588 hours of transmission, PTTs programmed in this way should have been able to transmit until 8 October 1997. The birds leave the spring staging areas during the last week of May (Clausen et al. 1999), arrive to breed in Svalbard between 5 June and late July (Madsen et al. 1989; Bregnballe & Madsen 1990), and return to their wintering areas in Denmark and England during September (Clausen & Fischer 1994; Percival & Evans 1997). Hence, this programming is able to secure (1) very detailed information about the birds' movements during spring migration and the pre-breeding period, (2) regular but less detailed information about the birds' (expectedly fewer) movements during the breeding and moulting periods, (3) and detailed information about the birds' post-breeding movements and autumn migration.

Signals transmitted by the PTTs were subsequently tracked by the ARGOS satellite system, and the calculated geographic locations of the birds, hereafter referred to as 'fixes', were down-

loaded by use of the PRV protocol via ftp-server (ARGOS 1996). The accuracy of fixes was provided by ARGOS in six location classes. Four classes are based on at least four received PTT messages: 3 (accuracy < 150 m), 2 (150–349 m), 1 (350–1000 m), 0 (> 1000 m). The other two, A and B, are based on three and two received messages, respectively, with no estimate of location accuracy.

The obtained fixes were plotted to maps by use of ArcView 3.0 software. The triangulation method used to calculate the locations of the birds results in two alternative possible positions (ARGOS 1996). 'Odd' fixes (fixes at 'impossible' locations, e.g. far out of normal range or too far away from previous or subsequent locations, recalling that the birds migrate with speeds of 70 to 90 km/hour, see introduction) were rejected. The alternative locations of rejected fixes were downloaded with the PRV/A protocol and accepted if they were within reasonable distance from previous or subsequent locations. These will be referred to as corrected fixes. The PRV/A protocol also provides additional fixes based on fewer satellite contacts (ARGOS 1996); three such additional fixes within reasonable distance from subsequent locations were also accepted by manual inspection.

Minimum distances travelled by migrating geese between subsequent fixes were calculated by use of the orthodrome equation of Imboden & Imboden (1972). The calculated orthodrome distances between fixes were summed to give the distance travelled during the whole flight from the wintering quarters to the breeding grounds. Migratory speed between two subsequent fixes may be calculated by dividing the orthodrome distance by the time used to travel between the two fixes. Migratory speeds calculated this way between fixes close together are, however, susceptible to small errors in position. To reduce this error, migratory speeds along the migratory track were calculated for each fix by dividing the orthodrome distances travelled between the previous and following fixes by the time used to travel between the three fixes.

Daily counts of the brent geese staging in the Agerø area were made from 16 May until 2 June 1997. The counted flocks were checked for ringed individuals and birds with PTTs, recognisable by their yellow abdomens, and whenever possible the colour ring combinations were read. The spring fattening condition of ringed individuals was

assessed by means of abdominal profile indices (method of Owen 1981, modified to a scale ranging from 1 to 4 for use on brent geese by R. Drent, unpubl. data).

It is known that while staging at Agerø, the brent geese roost communally during night northwest of Agerø, less than 2 km west of the catch site. The geese fly out in several flocks during the day to feed on salt marshes or *Zostera marina* beds. The birds roosting at Agerø disperse to sites up to 10 km north, southwest and southeast of Agerø (Clausen 1994). Assuming that none of the birds with PTTs left the Agerø area, it was possible with the fixes from ARGOS to check the reliability of the location classes. This was done by calculating the orthodrome distance from northwest Agerø to the location of each fix received during pre-migration.

Daily counts of northbound migrating brent geese were conducted at Lista (58°06'N 06°33'E), southwest Norway, by observers from Lista Fuglestation. The counts were made on a daily basis, from sunrise until noon.

Results

Pre-migration

From 17 May until the evening of 29 May 1997, when the geese were still staging in Denmark, a total of 99 fixes were received. The fixes were quite unevenly distributed between the five PTT marked birds, ranging from 40 fixes from 11601 to one fix from 11604. The locations of the fixes made a dot-scatter with outlying positions ranging from ca. 245 km west of Agerø and off the coast in the North Sea to ca. 175 km southeast of Agerø in southeastern Denmark (Fig. 1), but with a concentration of locations in the vicinity of Agerø. An analysis of distributions of the different locations classes revealed that (the few) fixes classified as location class 3, 2 or 1 all were less than 10 km away from the Agerø roost site, i.e. within the range normally used by the geese (Fig. 2). The majority of fixes (93% of those received) were, however, all in the less accurate location classes, 0, A and B. About half of the fixes with location class 0 and A were inside the normal range of the geese, while only 20% of the fixes

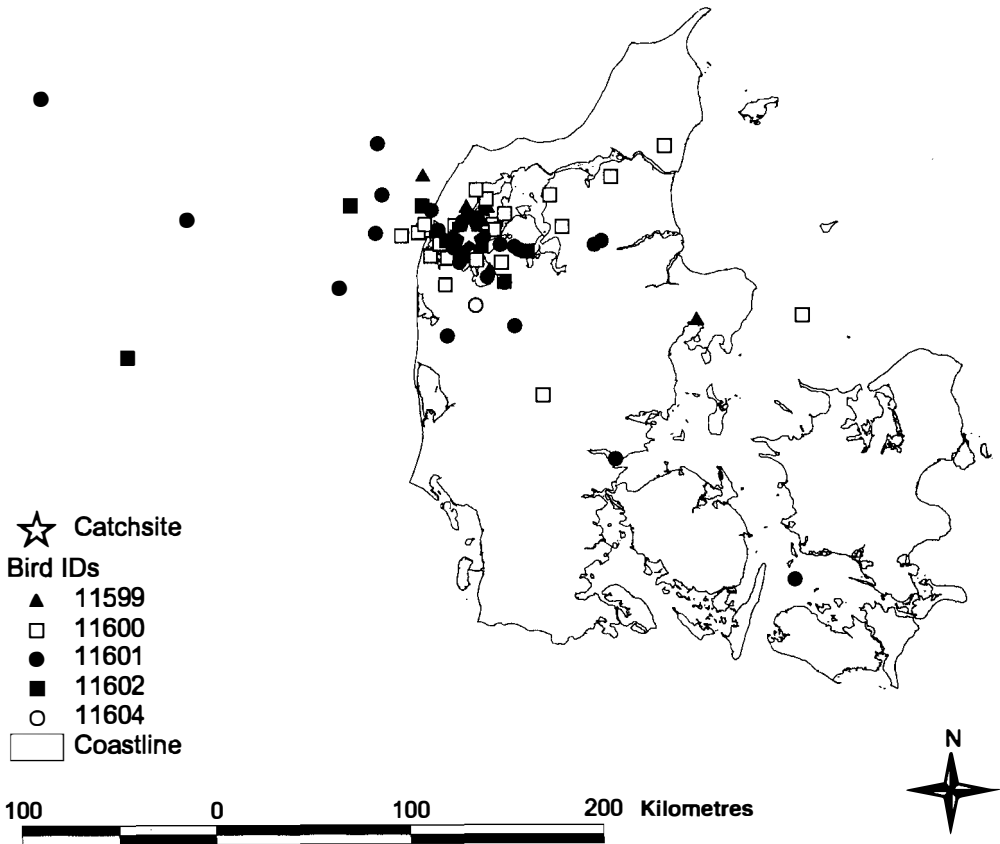


Fig. 1. Map of Denmark showing the position of fixes received prior to spring migration from five light-bellied brent geese equipped with satellite transmitters, 15 May–29 May 1997. Each bird is identified by its transmitter ID. The star highlights the site at Agerø where the brent geese were caught.

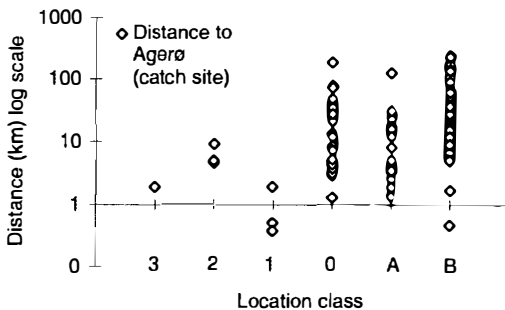


Fig. 2. Calculated orthodrome distances from the catch site at Agerø to the position of fixes received from the PTTs for different location class categories. The plot includes fixes received 15 May–29 May 1997 (see Fig. 1) when the satellite-tracked birds were staging in the immediate surroundings of Agerø.

classified as location class B were inside (Fig. 2, Table 1) Ground-based observations revealed that at least four of the birds with PTTs stayed in the immediate vicinity of the catch site on Agerø, i.e. 11599 (observed 26, 27 and 29 May), the paired birds 11600 and 11602 (observed 17, 20, 23, 24, 26 and 27 May), and 11604 (observed 23, 24 and 27 May). The remaining bird, 11601, was only observed once after it was marked, on 24 May. These observations, in combination with the received fixes and the subsequent tracking of spring migration (see below), do, however, confirm that all birds stayed in the Agerø vicinity until 28–29 May.

Table 1. Statistics on location class accuracy. The orthodrome distances between fix locations and the catch site at Agerø were calculated for each of the 99 fixes received prior to spring migration 15–29 May 1997.

Location class	Total no. of fixes	No. of fixes within 10 km from catch area	Distances away from catch site (km)			
			Minimum	Maximum	Mean	Median
3	1	1	1.93	–	–	–
2	3	3	4.60	9.19	6.23	4.91
1	3	3	0.38	1.95	0.94	0.51
0	23	10	1.29	187.19	29.26	13.63
A	25	14	1.34	125.42	14.40	5.07
B	44	9	0.48	245.17	47.39	24.07

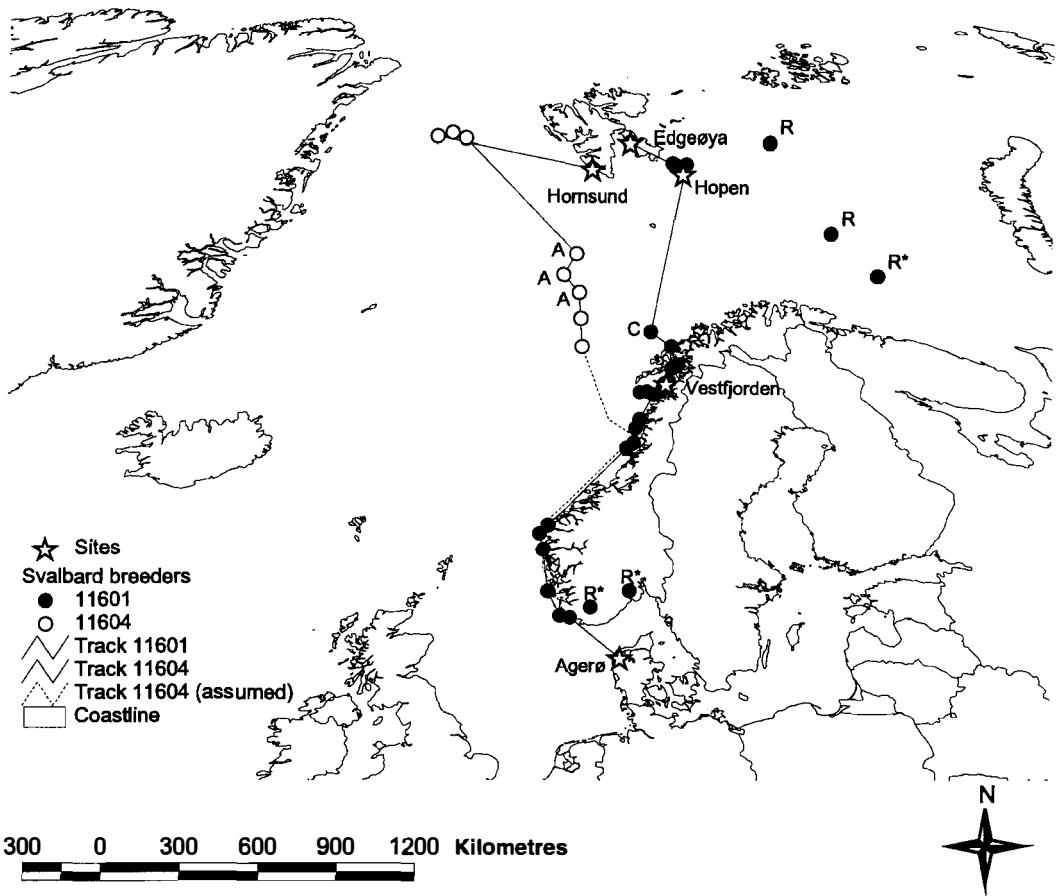


Fig. 3. Map showing migratory routes of two light-bellied brent geese tracked with satellite transmitters from 29–30 to May–1–2 June 1997. Each dot represents a fix received from the satellite transmitter, joined by lines to highlight the route followed by the birds. Stars and site names highlight sites where the birds stopped during their migration. Fixes marked R are rejected, as they would lead to unrealistic flight speeds between these and previous or subsequent fixes. Fixes marked C are corrected 'mirror' positions of rejected fixes which have been accepted as valid records and which are within realistic range from previous or subsequent fixes. Fixes marked A are additional fixes which have been accepted as valid records and are based on few satellite contacts, but within reasonable distance from previous fixes. Fixes marked R* are rejected records without a realistic mirror position.

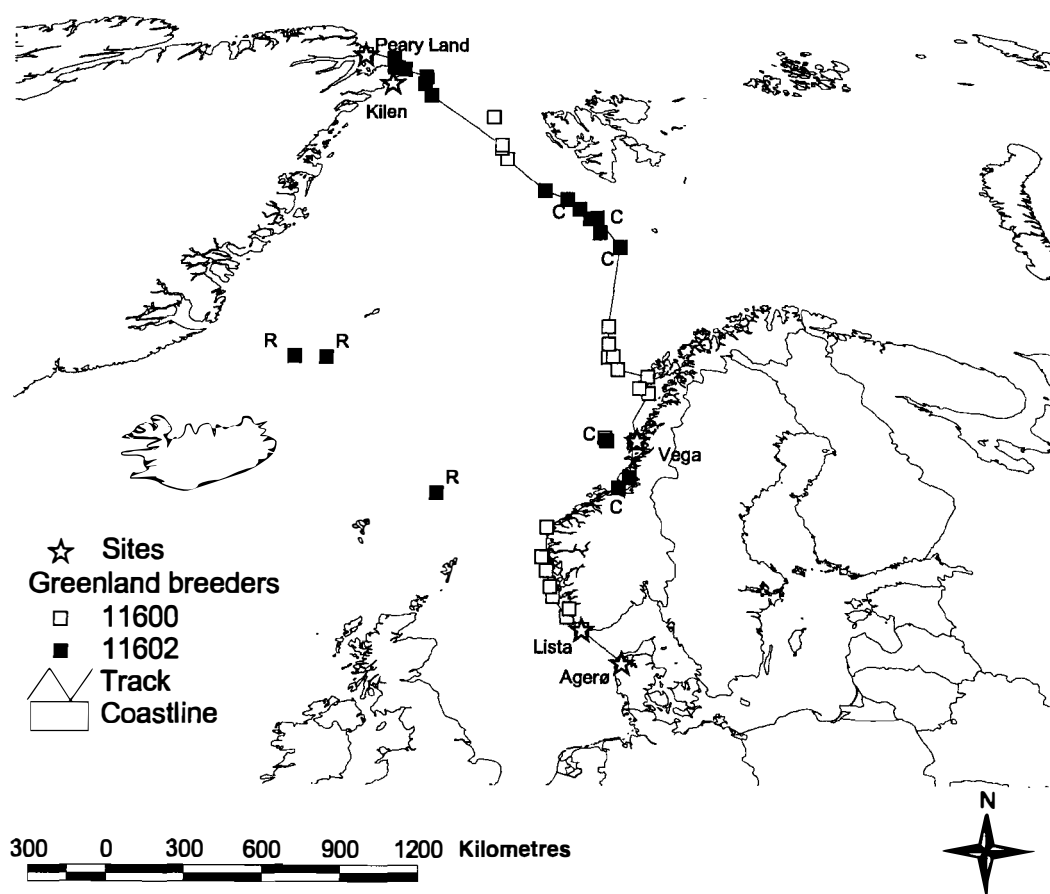


Fig. 4. Map showing the migratory route of two (paired) light-bellied brent geese tracked with satellite transmitters 30 May–2 June 1997. For further explanations, see Fig. 2.

Spring migration and pre-breeding staging

Four birds were tracked successfully to sites which may be considered as pre-breeding staging areas. Two birds, 11601 and 11604, migrated 'the expected route' from Denmark, along the western coast of Norway and up to Svalbard (Fig. 3), while the paired birds 11600 and 11602 migrated along the western coast of Norway and up to northern Greenland (Fig. 4).

Bird 11601 followed a track along the western coast of Norway, flew between Lofoten and the Norwegian mainland, and migrated north across the southern Barents Sea via Hopen to arrive on Edgeøya in southeast Svalbard (Fig. 3). The track was based on 23 fixes, with the rejection of three

fixes: two location class B fixes inland in southern Norway and one location class B fix northeast of Murmansk, which would require flight speeds of 194 to 529 km/hour between these and subsequent fixes, and with even more unrealistic flight speeds if the alternative positions were used.

The first fix on the migration track was received north of Lista, southeastern Norway, on 30 May 1997 09:07 UTC. Assuming that the bird would initiate its migration with a flight speed in the range of 60–70 km/hour, it would have left Agerø on 30 May in the morning between 5:12 and 5:45 UTC. The first fix from Edgeøya was received 3 June 12:09 UTC. However, this fix was the first one after the transmitter had been switched off for 17 hours, and the fix prior to this one was north of Hopen at 2 June 14:05 UTC (Fig. 5). Assuming

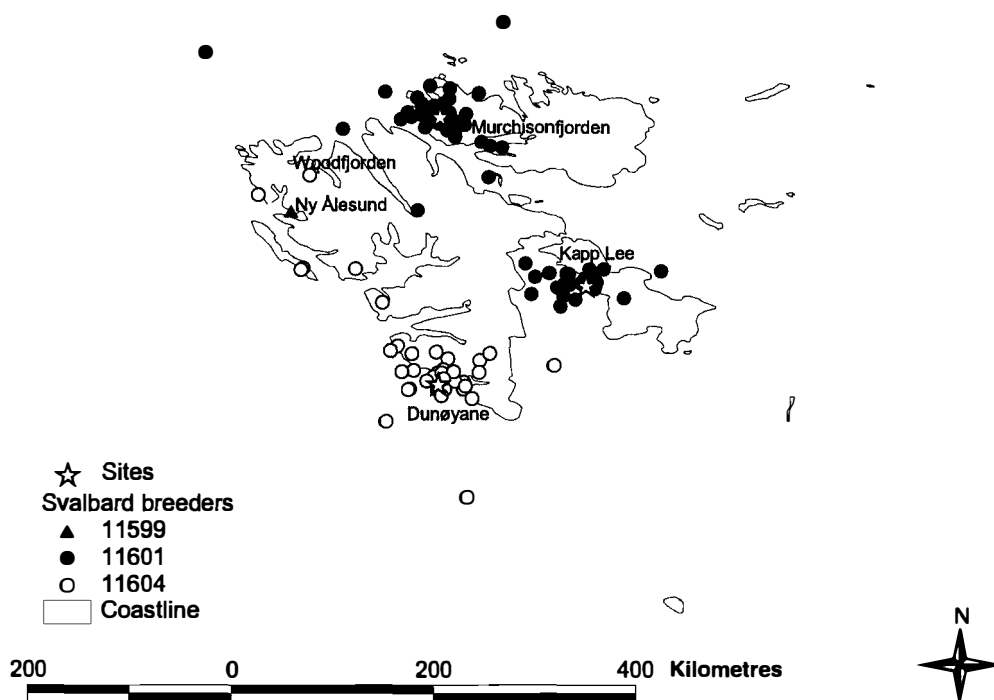


Fig. 5. Map of Svalbard showing the position of fixes received from two light-bellied brent geese with satellite transmitters (11601 and 11604) during the pre-breeding, breeding and/or moulting period 1 June–15 August 1997. One bird, seen on eastbound migration at Ny-Ålesund on 12 June (see discussion), is believed to be the bird with transmitter 11599, which had stopped sending signals.

that the last ca. 150 km from Hopen to Edgeøya may have been travelled in less than four hours, the bird travelled the distance from Agerø to Edgeøya between 30 May ca. 6:00 UTC and 2 June ca. 18:00 UTC, using 84 hours to complete the journey. The distance travelled by the bird was estimated at 2764 km (class 0–3 fixes) to 2824 km (all fixes except class B).

Once having arrived on Edgeøya, the bird stayed in this area five days (31 fixes, last fix received from this area 7 June 19:30 UTC). The average position of the most accurate fixes (4 fixes, location class 1) was 78°04'N 21°05'E, i.e. the bird stayed in the vicinity of Kapp Lee, northwestern Edgeøya (Fig. 5).

The track of bird 11604 was far less well described than that of 11601 because of poorer PTT performance. The first fix which gave evidence of migration was received from the Norwegian Sea at 69°40'N 9°16'E on 30 May 1997 17:23 UTC. From there the bird flew north across the southern Barents Sea (Fig. 3; based on 5 fixes 30 May 17:23 to 23:13 UTC, two class 0, and three

additional fixes). On 31 May, the bird was migrating in the Greenland Sea area, halfway between Greenland and Svalbard (Fig. 3; 3 fixes 31 May 17:02 to 18:43 UTC, class 0, A, and B). According to the longitudinal movement, the bird was migrating west, i.e. towards Greenland. The bird turned around, however, as the next fixes received from 1 June 14:59 UTC onwards came from southwest Spitsbergen (Fig. 5). Assuming that the bird followed a route similar to that of the other three birds tracked up to Vega (Figs. 3 and 4), and migrating from there over the sea up to the first position in the Norwegian Sea, with a flight speed in the range of 60–70 km/hour, it would have left Agerø at 29 May in the afternoon between 13:02 and 17:05 UTC. Hence the bird may have travelled the distance from Agerø to Spitsbergen between 29 May ca. 15:00 UTC and 1 June ca. 15:00 UTC, taking approximately 72 hours to complete the journey. The distance travelled by the bird, assuming the track via Vega, was estimated at 3272 km (class 0–3 fixes) to 3363 km (all fixes except class B).

The bird stayed in southwest Spitsbergen for eight days (33 fixes, last fix received from this area 9 June 22:10 UTC). The average position of the most accurate fixes (11 fixes, 10 location class 0 and 1 location class 1) was 77°00'N 14°56'E, i.e. the bird stayed in the vicinity of Dunøyane, off Hornsund (Fig. 5).

The paired birds 11600 and 11602 followed a track intermediate between those of 11601 and 11604. The transmitters of the two birds were out of phase as we received signals from either the one or the other during approximately 16 hours per day. The birds flew along the Norwegian coast to Lofoten; from there they flew west of Lofoten and northward over the southern Barents Sea; west of Bjørnøya they took a northwesterly route towards Peary Land, northern Greenland (Fig. 4; track based on 41 fixes). The first fix on the migration track was received ca. 70 km north of Lista, southeastern Norway on 30 May 1997 07:27 UTC. However, two birds with yellow dyed abdomens were observed migrating together on a northbound route by observers at Lista Fuglestasjon on 30 May 06:20 UTC; these must beyond doubt be birds 11600 and 11602 (migrating with 63 km/hour to the location of the first satellite fix).

Assuming that the birds would have initiated their migration with a flight speed in the range of 60–70 km/hour, they would have left Agerø on 30 May in the morning between 3:07 and 3:44 UTC. The first fix from Peary Land was received on 3 June 7:08 UTC. The fix prior to that one, located 90 km further east, was received on 2 June 22:38 UTC, which suggests that the birds would have arrived in Peary Land sometime in between. Assuming that the birds terminated their migration with a flight speed in the range of 30–40 km/hour (see below), they would have arrived in Peary Land on 3 June between 0:53 and 1:39 UTC. Hence the birds travelled the distance from Agerø to Peary Land between 30 May ca. 3:00 UTC and 3 June ca. 01:00 UTC, using 94 hours to complete the journey. The distance travelled by the birds was estimated at 3506 km (class 0–3 fixes) to 3642 km (all fixes except class B).

Once having arrived in Peary Land, the birds stayed for only two days (18 fixes, last fix received from this area 4 June 8:39 UTC). The average position of the most accurate fixes (2 fixes, location class 1) was 82°31'N 20°40'W, meaning that the birds stayed in the vicinity of Kap Eiler Rasmussen, southeast Peary Land (Fig. 6).

Timing of spring migration

Of the four tracked birds, one left Agerø on 29 May 1997 (afternoon) or earlier, and three 30 May (morning). Their departure from Denmark fits nicely with ground-based observations from Agerø as well as Lista. Around Agerø, 3300 light-bellied brent geese staged until 28 May 1997. On 29 May the number declined to 2900 birds; on 30 May 530 birds were left, and on 31 May only 237 birds remained there (Fig. 7). At Lista a total of 3089 light-bellied brent geese were recorded on northbound migration between 23 May and 11 June; the vast majority migrated on 30 May (2469 birds, 79.9%), and most of the remaining birds on 28, 29 and 31 May (total 440 birds, 14.2%) (Fig. 7).

Stops during spring migration

To assess whether or not the birds stopped along their migratory routes, we analysed the speeds at which the birds moved along their tracks. Due to the relatively poor performance of PTT 11604, we limited this approach to bird 11601 and the paired birds and only included fixes of location class 3-0 and A, excluding class B fixes.

Bird 11601 migrated north with migratory speeds ranging from 29 to 70 km/hour to approximately 68°N, where it stopped for at least 19½ hours from 31 May 1997 ca. 15:15 UTC to 1 June 10:45 UTC (Fig. 8). The average position of the two best fixes (location class 1) at 67°46'N 15°07'E suggest it stopped in Vestfjorden at the Norwegian coast inside Lofoten (Fig. 3). The apparent lowering of the speed with which the bird progressed from 62°N to 65°N between 30 May and 31 May (Fig. 8) suggests another stop at this more southerly latitude, but this can not be confirmed from fix locations, because the PTT was switched off during this part of migration. Further north, the birds apparently stopped at least three hours on 2 June from ca. 11:00 to ca. 14:00 UTC in the vicinity of the island Hopen, southeast of Svalbard (Figs. 3 and 8).

The paired birds 11600 and 11602 migrated north with migratory speeds ranging from 56 to 82 km/hour to approx. 66°N, where they stopped for at least 10½ hours on 31 May 1997 from ca. 6:20 to 17:00 UTC (Fig. 8). The average position of the three best fixes (location class 1) suggest

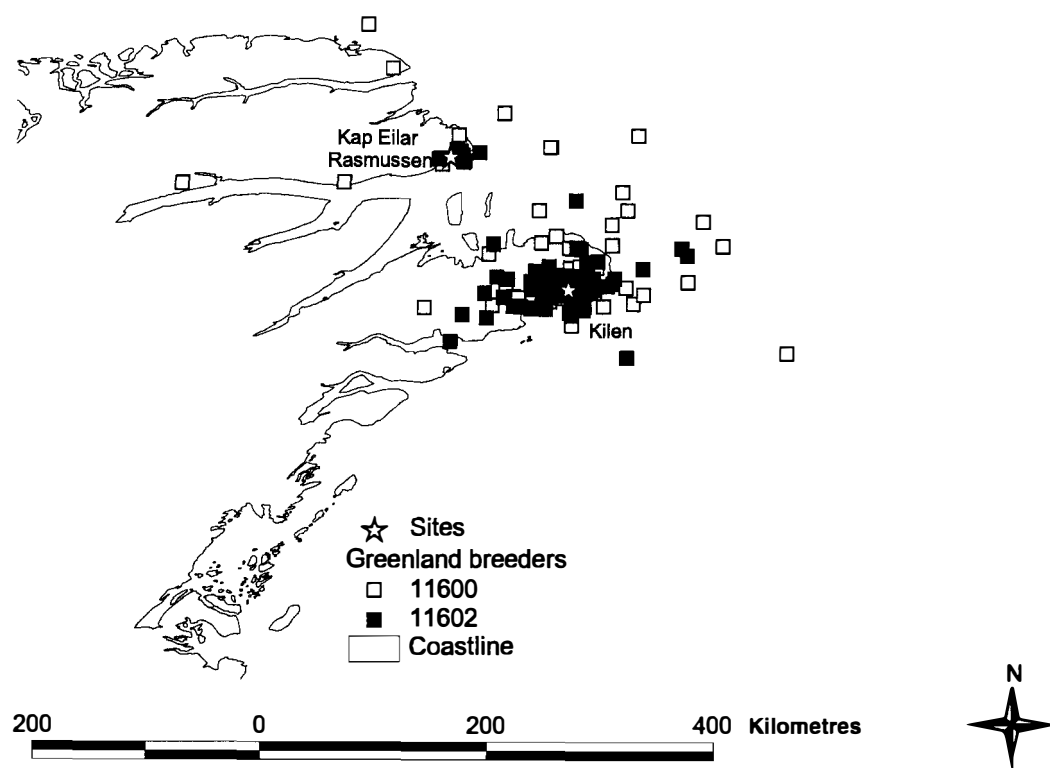


Fig. 6. Map of northeasternmost Greenland showing the position of fixes received during the pre-breeding, breeding and/or moulting period 1 June–15 August 1997, from a pair of light-bellied brent geese with satellite transmitters.

they stopped in the Norwegian Sea, 33 km west of Vega, at $65^{\circ}36'N$ $11^{\circ}02'E$ (Fig. 3). From there the birds apparently migrated with speeds ranging from 19 to 85 km/hour straight up to Peary Land (Fig. 8).

Breeding/moulting

After staging a few days in pre-breeding staging areas, the four satellite tracked birds moved to sites where they would have been breeding and/or moulting. Breeding (i.e. egg-laying, incubation of eggs, and rearing of goslings) takes place from 8 June through July (Madsen et al. 1989; Bregnballe & Madsen 1990), and moult is initiated from mid-July (non-breeders shed their flight feathers during 13–16 July and breeders during 21–24 July; Bregnballe & Madsen 1990), after which the birds are unable to fly for three weeks (Cramp &

Simmons 1977). Hence we consider fixes obtained from 8–10 June to 15 August as being from areas where the birds have bred or attempted to breed and/or have moulted.

Bird 11601 migrated north from Kapp Lee, Edgeøya, to the northwestern end of Nordaustlandet between 7 June 19:30 UTC and 8 June 17:27 UTC. From 8 June until 15 August the bird stayed in this area (Fig. 5; 90 fixes received). The average position of the four best fixes (3 location class 2 and 1 location class 3) at $80^{\circ}03'N$ $19^{\circ}03'E$ suggests the bird bred/moulted at Murchisonfjorden, Gustav V Land, Nordaustlandet.

Bird 11604 migrated north from Dunøyane, southern Spitsbergen, on 10 June. However, we only received six fixes (2 location class 0 and 4 location class B) during 10 and 11 June, after which the PTT stopped transmitting. The better fixes suggest a move from Dunøyane via Isfjorden to Woodfjorden.

The Greenland birds migrated southeast from

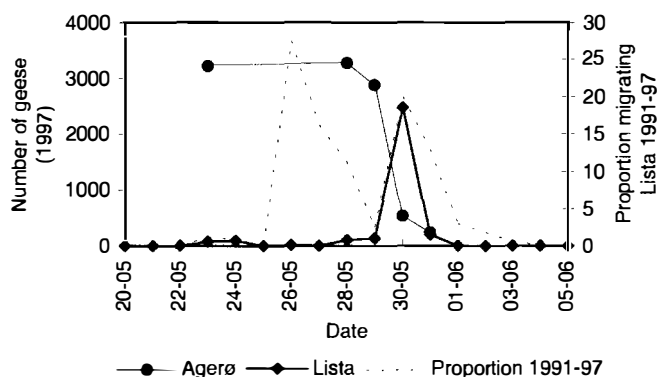


Fig. 7. Diagram showing the timing of spring migration of light-bellied brent geese. Numbers of brent geese counted at the spring staging area at Agerø and the daily number of brent geese observed on northbound migration at Lista in 1997 are presented. The proportion of all brent geese seen on spring migration at Lista during 1991–1997 is given for comparison.

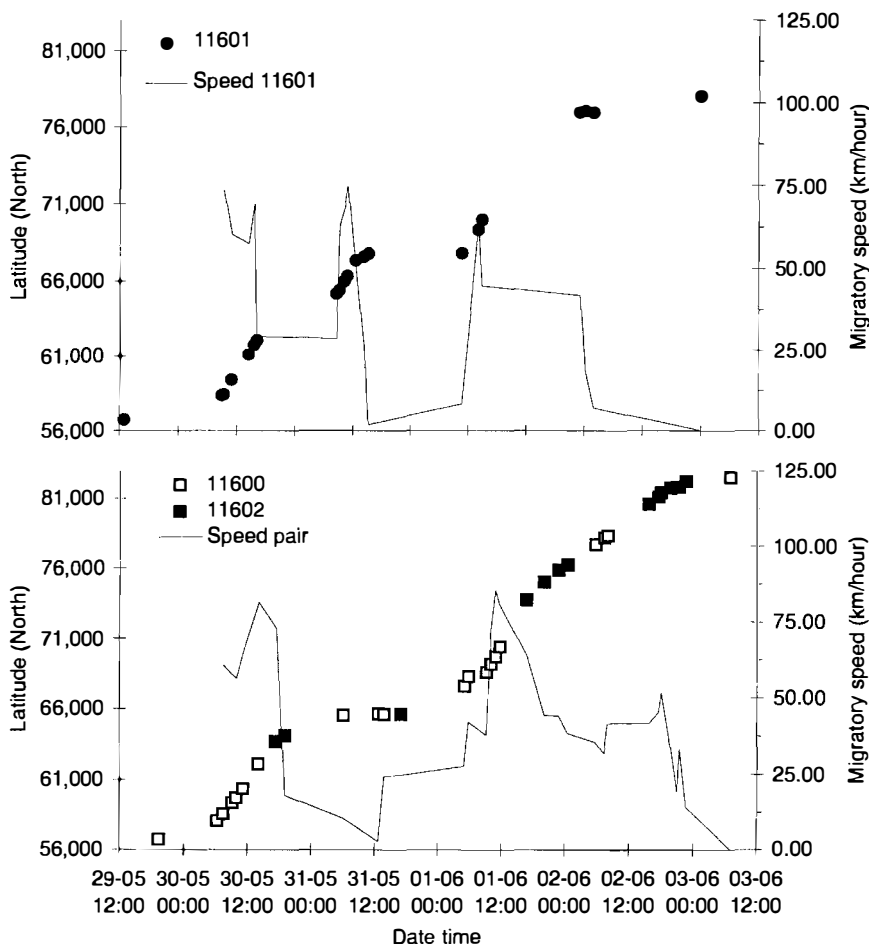


Fig. 8. Diagrams showing the latitudinal movements and calculated flightspeeds for three satellite-tracked light-bellied brent geese during their spring migration 30 May–2 June 1997.

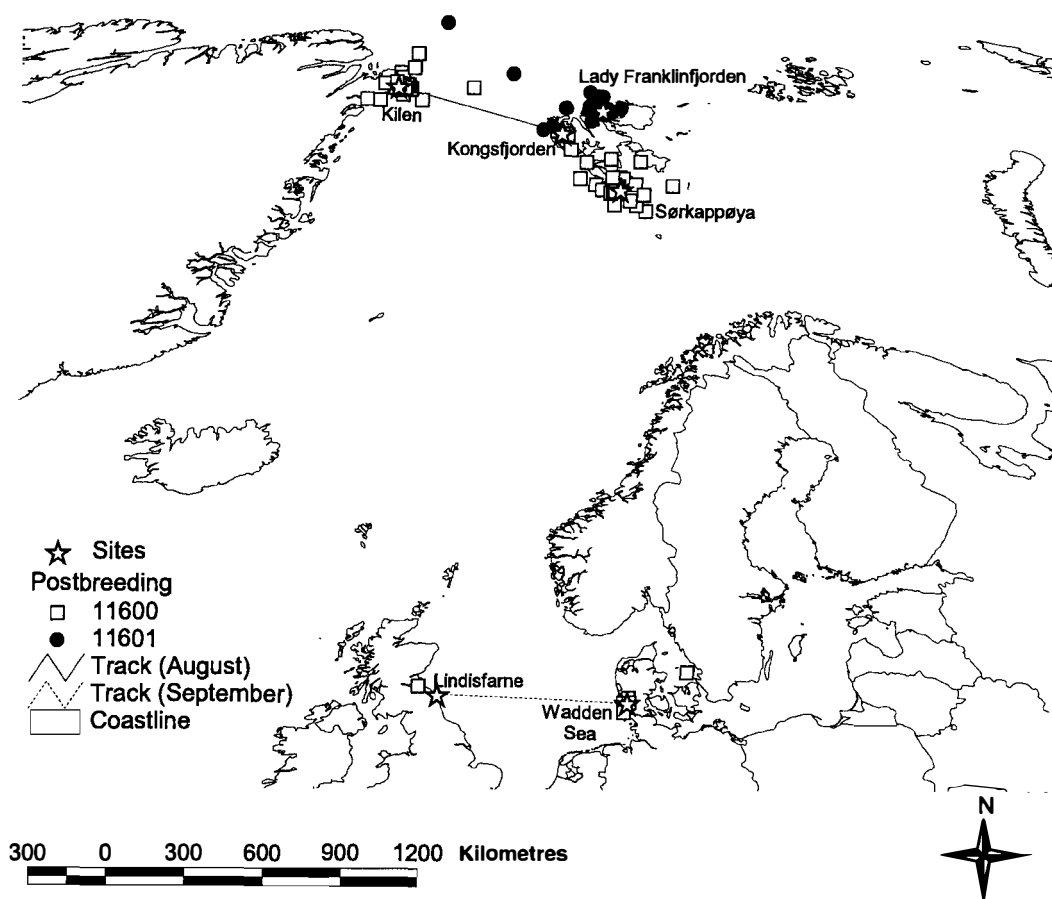


Fig. 9. Map showing the position of fixes received from two light-bellied brent geese tracked with satellite transmitters 16 August–29 September 1997. Parts of the migratory route followed by bird 11600 on return migration are highlighted by joining stars which indicate sites and site names where the birds stopped, but the route from Svalbard to the Wadden Sea is unknown. For further explanations, see Fig. 2.

Peary Land to Kilen, Kronprins Christian Land, on 4 June between 8:49 and 15:23 UTC, where they stayed until 15 August (Fig. 6; 203 fixes received). The average position of the seven best fixes (6 location class 2 and 1 location class 3) at $81^{\circ}11'N$ $13^{\circ}02'W$ suggests the birds bred/moulted on Kilen close to the coast of the Greenland Sea.

Post-moult staging and autumn migration

After breeding/moulting, only two of the transmitters were still active, i.e. 11600 and 11601.

Bird 11600 stayed another week in the Kilen area (41 fixes 16 to 22 August, last fix 22 August

10:03 UTC) before moving. On 23 August 1997 the bird had moved to northwest Svalbard (four fixes, three location class 0 and one class B). The average position of the location class 0 fixes suggests the bird was staging at $79^{\circ}05'N$ $12^{\circ}16'E$, i.e. at Kongsfjorden, west Spitsbergen (Fig. 9). The following fixes were received on 25 August, when the bird had moved further south to southernmost Svalbard, where it stayed from 25 August through to 8 September 1997 (41 fixes). The average position of seventeen location class 0 fixes ($76^{\circ}31'N$ $17^{\circ}04'E$) suggests the bird was staging at Sørkappøya, the southernmost island in the Svalbard archipelago (Fig. 9). During the period from 9 to 19 September no fixes were received from the bird. On 20 September 1997 a fix was

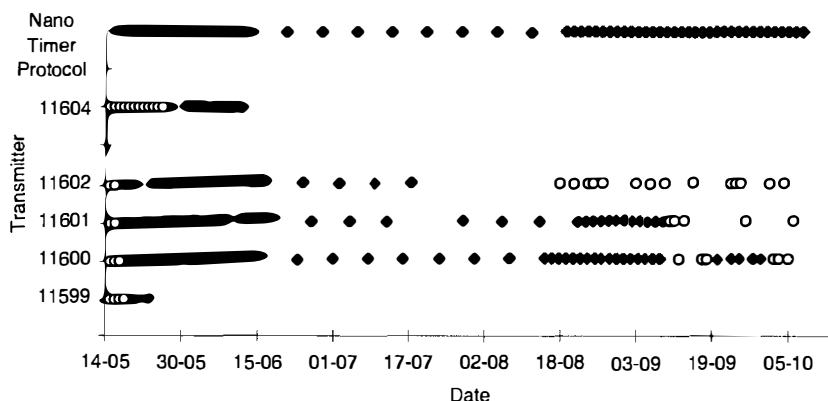


Fig. 10. Diagram showing the performance of the five satellite transmitters mounted to light-bellied brent geese in comparison with the ideal performance, based on the Nano Timer Protocol and a lifetime of 588 hours of transmission. Closed diamonds give dates when useable fixes were received; open circles give days when signals had been transmitted but location estimates could not be made, according to ARGOS PRV/A protocols.

received from the northern part of the Danish Wadden Sea, where the bird stayed until 27 September (Fig. 9, four fixes, one class A and three additional fixes from PRV/A protocol). On 29 September 1997 at 04:08 UTC the last fix (class B) was received from the transmitter at 75 km northwest of Lindisfarne, Northeast England (Fig. 9). The bird and its mate was observed by ground-based observers the same date at Lindisfarne at 19:00 UTC (M. Denny, pers. comm.).

Bird 11601 also stayed in the vicinity of its proposed breeding/moult area after moult. The received fixes (59 fixes 21 August to 8 September 1997) suggest the bird had moved east from its breeding/moult area. The average position of the four best fixes (two location class 1, one class 2 and one class 3) $80^{\circ}04'N$ $19^{\circ}35'E$ suggest the bird was staging at Lady Franklinfjorden, Nordaustlandet (Fig. 9).

Transmitter and attachment performance

The performance of the transmitters, i.e. results actually obtained in form of useful fixes, can be contrasted with the ideal situation that useable fixes would be received at least once every 8-hour cycle the transmitter was operating. With the estimated lifetime of 588 hours of operation, and the Nano Timer programming presented above, we should have been able to follow the birds daily between 15 May and 15 June, weekly between 16

June and 15 August, and every 1½ day between 16 August and 8 October 1997 (Fig. 10). The actual performance of the transmitters were, however, quite remote from this ideal performance. All five transmitters gave no reliable fixes on the first days after attachment, with the first useful fixes being available three (two birds), four, five and thirteen days after attachment (Fig. 10). The first transmitter (11599) stopped on 23 May 1997, prior to migration (Fig. 10); as the bird was observed in the field at Agerø on 26 and 27 May 1997, with the transmitter attached on its back, we can eliminate the possibility that the bird had lost its transmitter. The next transmitter (11604) stopped on 11 June 1997, just after the bird migrated up to northern Svalbard. The third transmitter (11602) gave regular fixes until 17 July 1997, when the bird probably would have started to moult; signals were also received from mid-August through to early October 1997, but none gave useful fixes (Fig. 10). The remaining two transmitters (11600 and 11601) both worked continuously until 8 September. After this date signals were received until 6 October 1997 (11601) and 5 October 1997 (11600), but only fixes received between 20 and 29 September from 11600 were useful (Fig. 10). Hence, we were not able to track any of the individuals on their complete return migration from Svalbard to the wintering areas in Denmark or England.

Two of the birds returned to Lindisfarne with the satellite transmitters attached. 11600 was observed with transmitter attached from 29 September to 21 October, and by 23 October

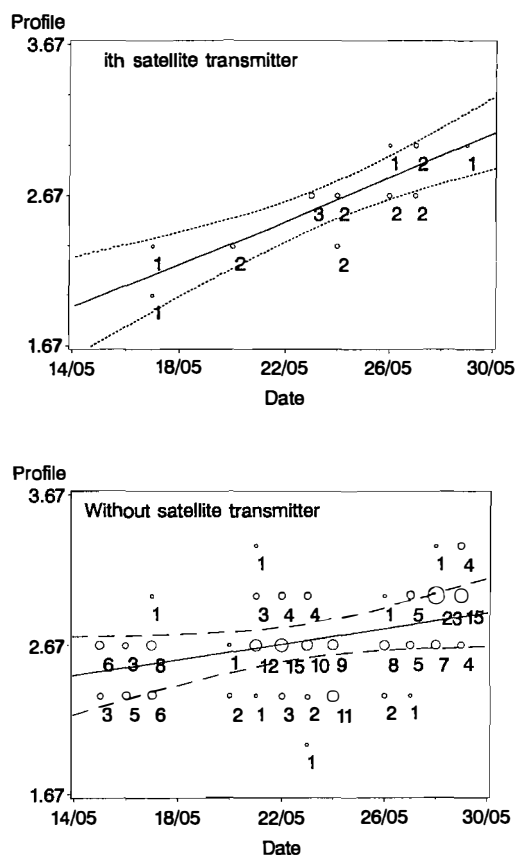


Fig. 11. Development in abdominal profile indices of brent geese with (upper) and without (lower) satellite transmitters attached 15–30 May 1997. The size of circles and the numbers depicts the number of individually recognisable birds classified to each profile index per day. Lines are simple linear regression models, fitted to the data (counting days from 15 May = 1), and hatched lines give 95% confidence limits of the regression. Birds with satellite transmitters: profile = $1.94 + 0.0679 \times \text{day}$; $r^2 = 0.68$, $P < 0.0001$. Birds without satellite transmitters: profile = $2.41 + 0.0321 \times \text{day}$; $r^2 = 0.28$, $P < 0.0001$.

1997 the transmitter was no longer attached. 11604 was observed with the transmitter attached between 4 and 24 October 1997, but had lost the transmitter on the following observation on 8 January 1998. 11601 still had the transmitter attached on 14 April 1998, only visible by the aerial antenna sticking out from the back feathers. The transmitter itself was not visible, having been completely preened under the surrounding feathers. The remaining two birds returned to the wintering areas without transmitters attached (details below).

Spring fattening, survival and breeding success of satellite-tagged individuals

The development in abdominal profiles of the satellite-tagged individuals from approximately score 2 immediately after capture to score 3 at departure (Fig. 11; One-way ANOVA, effect of days after 15 May, $F_{1,15} = 35.34$, $P < 0.0001$) shows that the birds gained weight after capture. Birds without satellite transmitters, but individually recognisable by colour rings, likewise increased in abdominal profiles from approximately score 2.4 immediately after capture to score 2.7 at departure (Fig. 11; One-way ANOVA, effect of days after 15 May, $F_{1,185} = 71.37$, $P < 0.0001$).

A comparison of the fitted linear regression lines actually revealed a significant difference between birds with and without satellite transmitters attached, the former developing faster in abdominal profiles. However, this result may have been caused by the lower abdominal profile indices of satellite tagged birds immediately after capture (Fig. 11), a result of the handling the birds had just been subjected to. A comparison of linear regression models based on a data set where data from the first four days after capture were excluded found no significant difference in development of abdominal profile indices. Hence it appears that birds with satellite transmitters developed abdominal profiles at a comparable or even better rate than birds without transmitters attached.

All birds fitted with satellite transmitters survived the attachment of transmitters. Four birds arrived to the wintering site in Lindisfarne: 11600 and 11602 (both observed five times between 29 September and 24 October 1997), 11604 (five observations between 4 October 1997 and 18 February 1998), and 11599 (observed 4 February 1998) (observations by M. Denny & G. Q. A. Anderson, pers. comm.). The fifth bird, 11601, was seen at Agerø on 31 March 1998 (P. Clausen). None of the birds came back with goslings, and 11601 and 11604 apparently returned without having mated.

Discussion

Due to the costs associated with purchasing PTTs

and using ARGOS satellite channels, satellite telemetry studies of migratory birds will usually be restricted to a few individuals. This leaves the investigator with the question of the significance of data obtained from a few focal birds in relation to the whole population. Despite this limitation, the present study has nevertheless answered several questions about the migratory movements and flyways of light-bellied brent geese in the north Atlantic.

Pre-breeding staging areas

The four tracked birds all migrated more or less directly to their first arctic destinations. The stopovers made by birds off Vega and in Vestfjorden were made in areas which, judged from maps, would be too deep to supply any submerged or intertidal food supplies, but which apparently must have been used for resting and drinking instead of feeding. After their arrival in the arctic, all the birds spent from two to eight days in pre-breeding staging areas before moving further to breeding and/or moulting sites. This confirms the existence of pre-breeding staging areas proposed by Clausen et al. (1999). The existence of pre-breeding staging areas is further supported by field observations from Svalbard. A flock of 50–60 light-bellied brent geese, including one bird marked on Agerø 15 May 1997 (red darvic AL), was observed feeding on the tundra near Vårsofbukta 77°40'N 14°20'E, in Bellsund, on 31 May 1997 (Bjørn Frantzen, pers. comm.).

Judged from maps of Svalbard and northern Greenland, the three pre-breeding staging sites used by the satellite tracked birds may be characterised as fairly large glacier-free areas. The same characteristic applies to sites used by other flocks of light-bellied brent geese observed in the pre-breeding period on Bjørnøya and Svalbard (Mehlum 1998, this volume). It is likely that vegetation growth in these areas starts slightly earlier than on many of the areas used for breeding and moulting further north and east, and the birds can use the sites for refuelling a few days, before continuing their migration to breeding or moulting areas, but this suggestion needs verification from field studies.

Even though the studied birds did not stop to feed along the Norwegian coast, we can not exclude the possibility that in some years some

birds may stop for more days to feed. The migration in 1997 was quite delayed. In other years the birds migrated already between 23 May and 27 May (Fig. 7), and the observations from Lista during spring 1991 remain specially puzzling. In 1991, 236 birds were counted on north-bound migration off Lista already between 21 April and 11 May (Clausen et al. 1999) and it is unlikely they could have found any snowfree areas on Svalbard so early.

Breeding, moulting and post-moulting distributions

The two birds which moved further north in Svalbard continued on to areas which are known as both breeding and moulting areas (11601 to Murchisonfjorden and 11604 to Woodfjorden) (Clausen et al. 1999). A hitherto unnoticed northward migration of brent geese over Ny-Ålesund 78°55'N 12°00'E was also recorded in the spring of 1997 (F. Mehlum, pers. comm.). Several small flocks were seen on 11 June, and among these rings were read on two birds (light green darvics BX and DN), both immatures born in 1996 and marked in Lindisfarne in February 1997. In addition, a direct observation was made of a bird with yellow abdomen and satellite transmitter on its back. This bird was seen flying eastward over Ny-Ålesund on 12 June 17:25 UTC (F. Mehlum, pers. comm.). This timing suggests that this was the immature bird marked with transmitter 11599 (Fig. 5) because 11604 had already migrated north to Woodfjorden between 10 June 20:55 and 11 June 15:47 UTC. Brent geese start breeding when two years old (Cramp & Simmons 1977), and the evidence that at least three individually recognisable immatures travelled north along the west-Spitsbergen route suggests this to be an important route for non-breeders bound for moulting destinations in northern Svalbard.

The migration of birds north to Greenland confirms the existence of a link between the population breeding on Kilen and those breeding in Svalbard and Franz Josef Land. Hjort et al. (1987) has earlier suggested that the Kilen birds belong to the Svalbard population because the distance from Kilen to Svalbard (ca. 500 km) is much shorter than the distance to the nearest known breeding areas in Arctic Canada. The existence of the link was further supported by

the evidence obtained from bird 11600 that bred or moulted in Greenland and after moulting moved to a staging area in Svalbard.

Reassessment of North Atlantic light-bellied brent goose flyways

The now established link between the northern Greenland and Svalbard breeding populations represents a change in the traditional view of the North Atlantic flyways of light-bellied brent geese. Traditionally the northern Greenland breeding birds have been linked to the population which breeds in Arctic Canada and migrates over Greenland via Iceland to winter in Ireland (Salomonsen 1958). The link between birds that breed in arctic Canada, stage in Iceland and winter in Ireland is well established from ringing recoveries (review in Merne et al. 1999), and the same applies to birds which migrate along the western coast of Greenland and birds which cross southern Greenland (Gudmundsson et al. 1995; Boertmann et al. 1998). There is some evidence that the former breeding population in northern Greenland migrated down both the eastern and the western coasts of Greenland (Salomonsen 1950), but there is a lack of migratory observations in eastern Greenland from recent years (Melfotte 1975, 1976; Hjort 1995). In older Icelandic literature there is also evidence that flocks of brent geese occurred in parts of northern Iceland, but this is not the case today (Aevar Petersen, pers. comm.). One may speculate that these birds may have originated in Greenland and migrated via eastern Greenland and northern Iceland to winter in Ireland. The population using this route may have become extinct, or at least it may have been reduced to insignificant numbers, when all the North Atlantic brent goose populations declined in the 1930s and 1940s (reviewed in Salomonsen 1958). Later, with the recent increase in the Svalbard breeding population (Clausen et al. 1998), birds may have been moving away from Svalbard to breed in other areas because many of their former breeding areas now appear to be occupied by barnacle geese *Branta leucopsis* (Madsen et al. 1989). The migratory route used by the brent geese from Denmark to Greenland certainly suggests that these birds follow a track comparable to that of the Svalbard breeders, and only in the latter part

of their migratory route do they deviate from the Svalbard breeders by turning northwest towards Greenland.

There are no recent counts of the size of the population breeding in Kilen. In 1985, 850 birds were found in this area (Hjort et al. 1987), and this is by far the most important brent goose breeding site in northern Greenland today; however, scattered pairs have also been found breeding in sites north as well as south of Kilen (Hjort 1995). Hjort (1995) estimated the total northern Greenlandic population to be 1000 birds. This would account for ca. 20% of the population of light-bellied brent geese now known to be breeding in Greenland, Svalbard and Franz Josef Land, a population that has been fluctuating around 5000 individuals in the 1990s (Clausen et al. 1998).

Transmitter performance and transmitter impacts on birds

Despite the fact that several good data were obtained during this study, transmitter performance may still be considered to be relatively poor. If we take the ideal criteria that at least one useful fix should be available per 8-hour transmission cycle and that we should have transmission over 588 hours, the performance of the transmitters ranged from 80 hours to 432 active hours (14 to 74% with an average of 50%). As we know that all satellite-tracked birds survived, we can exclude the possibility that the birds had died or been taken by fox, etc., which could lower the performance. Hence the poor performance may be related to either technical problems or to loss of the transmitters.

Technical problems most likely account for the poor performance of the two transmitters that switched off earliest because both birds were subsequently observed with the transmitters attached (11599, transmitter stopped 23 May, bird observed on 26 and 27 May at Agerø, and probably on 12 June at Ny-Ålesund with transmitter attached; 11604, transmitter stopped 11 June, bird observed from 4 to 24 October 1997 at Lindisfarne with transmitter attached). The third transmitter stopped in mid-July, which could be due to transmitter loss as the bird was observed without transmitter immediately after arrival to Lindisfarne on 29 September. The remaining two transmitters performed almost

throughout the expected life period and may have stopped due to battery exhaustion as both birds were later seen with the transmitters attached to their backs.

The attachment method applied worked as planned. At least four (probably all five) birds migrated with their transmitters up to the breeding areas and did so during mass migration—i.e. at the same time as the rest of the population. This is in agreement with the study of Ward & Flint (1995), who found that female black brant *Branta bernicla nigricans* supplied with harness-attached transmitters ranging from 26 to 35 g migrated in due time together with the rest of the population, but they did not breed. None of the birds we studied bred either, but the significance of this observation is rather poor as only 23.5% of the potential breeders in the whole population bred in 1997 (Madsen et al. 1998, this volume). The missing breeding output could not be related to a poorer spring fattening condition of the birds with transmitters attached (Fig. 11).

The quality of received fixes was rather poor, with the vast majority being of class 0, A and B (exemplified by data from the pre-migration period in Table 1). A similar result was obtained in the study of lesser white-fronted geese (Lorentsen et al. 1998). The poor quality may partly be due to the fact that the birds were ground-based through most of the study because the quality of signals improve with flight heights. The results from the comparison of location class accuracy with likely positions within the Agerø staging area (Table 1) suggest that A fixes are of comparable quality to class 0 fixes, whereas class B fixes are so poor that they only after manual inspection may be used in long-distance trackings. For studies of local movements, both class 0, B and A fixes are of very low value, and it is an obvious goal for transmitter manufacturers to improve power outputs from these very small transmitters in order to improve future satellite tracking studies.

At any rate, the overall performance of the transmitters was far better than that of the transmitters fitted to Icelandic light-bellied brent geese in 1992–93 (Benvenuti 1993; Gudmundsson et al. 1995). None of these birds was tracked to the breeding grounds, and several birds were not even tracked over the ice-cap of southern Greenland. Whether or not this was due to a poor PTT performance, the burden of the relatively heavier transmitter (57 g + harness 18 g), or the teflon harness used remains unknown.

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Changes in distribution and habitat use of Svalbard light-bellied brent geese *Branta bernicla hrota*, 1980–1995: Driven by *Zostera* availability?

PREBEN CLAUSEN and STEVE M. PERCIVAL



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The Svalbard breeding population of light-bellied brent geese which winters in Denmark and at Lindisfarne, England, changed distribution and habitat use within all six areas used during the 1980s and colonised two new areas during the late 1980s and one during the early 1990s. There appeared to be two major causes of these changes: (1) the reduction or even disappearance of *Zostera* beds in four of the traditionally used areas, due to increased eutrophication and probably also changes in sedimentation processes, following constructions of barrages at Mariager Fjord and a causeway at Lindisfarne; and (2) the remaining beds of *Zostera* apparently have been depleted more rapidly in autumn and winter partly as a result of increased goose site use. In addition comes the cessation of cattle grazing and hay cutting of salt marshes in the formerly most important spring staging area. These changes have led to increased use of other areas and the establishment of three new areas of international importance for this brent goose population. The implications of the new patterns of dispersal are discussed in relation to future management of the areas used by the brent geese. Recommendations include improved management of salt marshes throughout their range and preparation of an international conservation plan.

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Introduction

The small and vulnerable Svalbard breeding population of light-bellied brent geese *Branta bernicla hrota* winters in Denmark and at Lindisfarne in Northeast England (Madsen 1984, 1987). The population has been censused regularly since the 1960s (Fog 1967, 1972; Madsen 1984, 1987; Clausen et al. 1998). Compared to the Siberian dark-bellied brent goose *Branta b. bernicla* population, the light-bellied brent goose population has shown a less pronounced increase in numbers following the shooting ban in Denmark in 1972. The dark-bellied population increased at a rate of 17% during the 1970s and 4% in the 1980s (Summers & Underhill 1991), whereas the light-bellied population increased at a rate of 7% during the 1970s and 7% during the 1980s (Clausen et al. 1998). The light-bellied population has, however, not recovered to its suggested size of >50,000 individuals early this century (cf. Madsen 1987).

Throughout the 1960s and 1970s, *Zostera* beds and salt marshes were the only habitats used by the brent geese (Fog 1967, 1972; Jepsen 1967, 1984; Madsen 1984, 1986). Based on observations in 1980–1983, Madsen (1984, 1986, 1987) described the development, distribution and habitat choice of the population and argued that eutrophication and salt marsh reclamation might have had a negative impact on the population development since the 1960s, hence causing the less pronounced development of the light-bellied brent goose population. Alternatively, problems should be looked for in the breeding grounds. An updated synthesis of the latter is given by Madsen et al. (1998, this volume).

Eutrophication can influence the growth of *Zostera* and other submerged macrophytes. This is because increased levels of nutrients often induce heavy colonisation by epiphytic algae growing on the plants and severe growth of phytoplankton populations in the water above the plants. Both the epiphytes and phytoplankton

reduce the light available for the macrophytes and thereby also reduce their growth. Consequently the macrophytes may disappear in severely eutrophicated areas (Borum et al. 1990; Sand-Jensen & Borum 1991; Valiela et al. 1992).

Salt marshes are present in all areas used by the brent geese (this study), but they are only of value for the geese when the sward is kept low by appropriate grazing pressure (e.g. Summers & Critchley 1990). The low sward is maintained by sheep or cattle grazing or mowing (e.g. Cadwalldr & Morley 1973). If unmanaged, the salt-marsh vegetation grows tall, large amounts of dead plant material accumulates (Bakker 1978; Lorenzen & Madsen 1985), and food plants favoured by the brent geese (e.g. *Puccinellia maritima*, *Plantago maritima* and *Triglochin maritima*, Boudewijn 1984) are replaced by other plants such as *Halimione portulacoides* and *Artemisia maritima* (Jensen 1985) or in the very brackish Danish fjords, reed *Phragmites australis* (Jepsen 1984).

Detailed studies were conducted in Denmark and at Lindisfarne in 1988–93 which aimed at

improving knowledge about the habitat use and feeding ecology of the light-bellied brent geese. This should make it possible to explore whether problems associated with eutrophication and/or salt-marsh management might be the cause of a reduction in the birds' food supplies at critical periods through the wintering period. In a previous paper, Clausen et al. (1998) reviewed the population development and changes in winter site use (i.e. numbers of geese and their phenology) by the light-bellied brent geese during the period 1980–1995. In this paper we review evidence of changes in habitat availability within the wintering areas used by the light-bellied brent geese. We also review how the geese have responded to observed changes. The paper gives an account of changes in goose site use and feeding habitat availability for each wintering area, followed by an area specific discussion of the observed changes in relation to eutrophication of estuaries, salt-marsh management, and carrying capacities of each area. The paper concludes with a general discussion of the changed *Zostera* availability in the wintering range

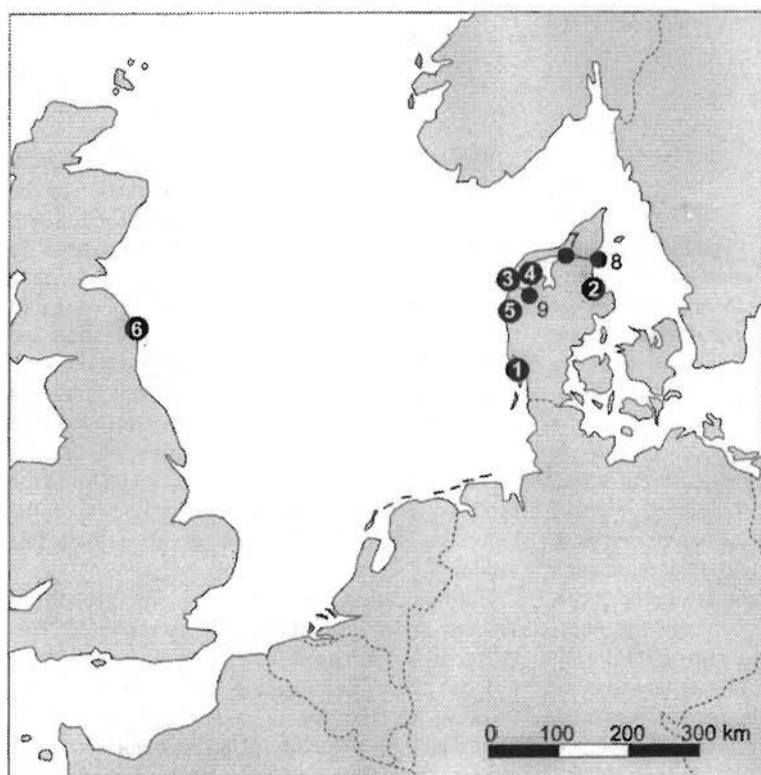


Fig. 1. Positions of the six sites used regularly by light-bellied brent geese within the last two decades: (1) the Danish Wadden Sea, (2) Mariager and Randers fjords, (3) Nissum Bredning; (4) the Agerø area, (5) Nissum Fjord, (6) Lindisfarne, as well as three new sites taken in use in the late 1980s and early 1990s, (7) Nibe and Gjølbredninger, (8) the Northern Kattegat coast, and (9) Venø.

and proposals for improved management of the population are put forward.

Materials and methods

Wintering areas and phenology

During the 1970s and early 1980s the light-bellied brent goose population made a successional use of six areas (Fig. 1) (Madsen 1984). The Danish Wadden Sea was used in autumn, followed by Mariager and Randers fjords in winter, but the geese switched to Lindisfarne during cold winters. In late winter the birds moved to Nissum Bredning, and from here split between Nissum Fjord and Agerø, the two spring haunts (Madsen 1984). During the 1980s the geese altered this migration pattern, especially with regard to phenology (see Clausen et al. 1998 for details). Furthermore the geese began to use two additional areas in Denmark during the 1980s (Clausen et al. 1998). In summary, compared to 1980–83, the staging period of the brent geese in the Wadden Sea was one or two months shorter in 1988–95. Consequently, the majority of the brent geese arrived one or two months earlier at Mariager and Randers fjords. At the other end of the staging period at Mariager and Randers fjords, a few hundred brent geese departed in December (peak occurrence period from 1980 to 1983) to Agerø, Nissum Bredning and the two new areas, Nibe and Gjørl bredninger and the Northern Kattegat coast (Fig. 1). The rest of the geese departed in February, one or two months earlier than in 1980–83. At Lindisfarne, a similar pattern emerged. The geese arrived in early September and departed in February in 1988–95, one month earlier than in 1980–83. Peak numbers occurred in December in 1988–95, one month earlier than in 1980–83. In Northwest Jutland the change has been most obvious around Agerø. In 1980–83, Agerø was only used in the spring; now it is used from November throughout the winter and spring until the departure for the breeding areas in late May. Recently another area has been used in Northwest Jutland, Venø, a small island 16 km southeast of Agerø (Fig. 1) (Clausen et al. 1999).

Goose counts, distribution, and habitat use

Detailed counts of light-bellied brent geese were made on at least a monthly basis throughout 1980–95 at the five most important Danish staging areas and at Lindisfarne (for details, see Clausen et al. 1998). In addition, observers in Denmark were asked to carefully draw the locations of all observed flocks of geese on maps (scale 1:25,000) and take detailed notes on habitat choice during 1980/81–1982/83 (Madsen 1986) and since 1988/89 (Clausen 1994). For some areas, mappings as well as details on habitat use are available for one or more of the years in between the two periods. Two of the three new areas used by light-bellied brent geese in the late 1980s and early 1990s, the Northern Kattegat coast and Venø, had been counted regularly by local observers throughout 1980–95. The third new site, Nibe and Gjørl bredninger, had been covered by professional observers in connection with a research programme carried out by the National Environmental Research Institute in 1985–95 (Madsen 1998a, 1998b).

The use of areas and habitats is expressed as numbers of goose-days. The number of goose-days between two counts is calculated as the average number of birds observed at the two counts multiplied by the number of days between counts; the calculated number of goose-days are then summed over the season for each area or habitat.

Food supplies and feeding performance

Light-bellied brent geese staging in Denmark outside the Wadden Sea usually feed on submerged macrophytes and salt-marsh halophytes (Clausen 1994); in the Danish Wadden Sea and at Lindisfarne they mainly feed on intertidal *Zostera* spp. and *Enteromorpha* spp. (Clausen & Fischer 1994; Percival et al. 1996; Percival & Evans 1997).

Monitoring of submerged macrophyte stands has been carried out irregularly by the Danish County Councils in most of the areas used by light-bellied brent geese in Denmark. The method applied has usually been a combination of aerial photographs and field observations. Field observations were made either from a boat or by wading along permanent transects where abundance and

depth ranges of individual plant species were recorded. The eutrophication status of the areas was evaluated by the presence/absence of eutrophication indications such as high nutrient levels, high concentrations of phytoplankton or epiphytic algae on rooted macrophytes in the surveyed areas, as well as algae blooms of *Ulva lactuca*, *Enteromorpha* spp., *Cladophora* spp. and other filamentous algae. Occasionally detailed mappings of the distribution of *Zostera* and *Ruppia* species have been made.

Additionally, we also mapped macrophyte distribution in the Wadden Sea (Clausen & Fischer 1994), in Mariager and Randers fjords (Clausen 1990), around Agerø (Drachmann et al. 1993), at Lindisfarne (Percival et al. 1996; Percival & Evans 1997), and in Nissum Bredning (Clausen et al. 1996). It must be noted that the available historical record of macrophyte distribution in the areas used by the brent geese is of varying quality. We can therefore only make rough comparisons for some areas, whereas firmer conclusions can be drawn regarding other areas.

Madsen (1988) showed that declines in *Zostera* supplies on intertidal mud flats in the Wadden Sea had several effects on the feeding behaviour of dark-bellied brent geese. When *Zostera* supplies dropped, feeding bouts (measured as the time of uninterrupted feeding with the head below the level of the shoulder), pace rates (time it took a feeding bird to take 10 steps), and dropping rates (number of droppings per hour) also declined. Madsen also found that the percentage *Zostera* cover of the mud-flat surface (assessed by visual observation) gave a reasonable estimate of available biomass. In the Wadden Sea and at Lindisfarne we also used some of these parameters as indicators of available food densities. In the Wadden Sea, plant cover was scored and feeding bout lengths were measured at some of the primary feeding areas for light-bellied brent geese (see Clausen & Fischer 1994 for details). At Lindisfarne plant cover, pace rates and dropping rates (by use of the method of Bédard & Gauthier 1986), were scored. Plant cover was calibrated to biomass by sampling *Zostera* and *Enteromorpha* in areas where the percentage cover was also assessed by visual observation. Samples were sorted into above- and below-ground materials of *Zostera* spp. and *Enteromorpha* spp. thalli, dried to constant weight at 60°C, and weighed (see Percival et al. 1996; Percival & Evans 1997 for details). In Mariager Fjord samples of seagrasses

were collected in the *Ruppia* dominated community (found at depths from ca. 30 to 80 cm) as well as in the *Zostera marina* bed (at depths from ca. 90 to 200 cm) in the main feeding area, Ajstrup Bugt (cf. Fig. 5). Both in October and November 1993 four samples were taken from each of four *Ruppia*-dominated plots and from the *Zostera* bed. Samples in *Ruppia* stands were taken by pressing a 15 cm wide circular plastic tube 10 cm down in the sediment and then digging out the sediment and plants found within the tube. In the *Zostera* area, a 0.1 m² square steel frame was placed by a scuba diver at the bottom. *Zostera* plants growing inside the frame that had been pushed down to the bottom when the frame was placed were then gently pulled inside the frame; plants growing outside the frame were likewise pulled outside. A square of *Zostera* turf was then cut along the inside of the frame, and the whole turf was taken to the surface in a sieve. All samples were washed in saltwater in the sieve (1 mm mesh size), and the material retained by sieving was stored in plastic bags. In the laboratory, samples from the *Ruppia*-dominated stands were sorted into *Ruppia* spp., *Zannichellia* spp. and *Z. marina*. Samples from the *Zostera* bed were sorted into above- and below-ground live material, the dead fraction being discarded, and the number of vegetative shoots counted. The length of all leaves from 15 vegetative *Z. marina* shoots were chosen at random and measured. All fractions were then dried to constant weight at 70°C and weighed. In the *Zostera* bed, most of the *Zostera* is inaccessible to feeding brent geese because *Zostera* grows at depths >90 cm, and brent geese can only reach 40 cm below surface. The actually available fraction of *Zostera* was therefore modelled by use of the *Zostera* availability model, developed in Clausen (1994).

Data on the present grazing and mowing status of all salt marshes within the areas were collected in 1992–93 by scoring the marshes to three levels of quality: (1) well-managed—grazing and/or mowing resulting in a short sward, less than five cm high throughout; (2) poorly managed—some grazing and/or mowing, but with uneven intensity resulting in tall vegetation over large parts of the salt marsh; and (3) unmanaged—overgrown but potentially useful for the geese if managed, i.e. *Puccinellia* or *Juncus/Festuca* marsh. The area of individual salt marshes was measured from maps (scale 1:25,000). Unmanaged *Halimione* and *Spartina* marshes, of little relevance for the geese

as foraging habitat, were omitted from the analysis.

Estimation of carrying capacities of salt marshes for spring fattening

The spring fattening period is of crucial importance for the breeding success of the brent geese (Ebbinge 1989). Ebbinge (1992) found the carrying capacity of grazed salt marshes for spring staging brent geese to be approximately 30 brent geese per hectare of grazed salt marsh, about three times as high as for unmanaged salt marshes. Based on these figures we calculated estimates of the carrying capacity of salt marshes the light-bellied brent geese use in spring in Denmark. We assumed that the Danish salt marshes could support 30 geese per ha on well-managed salt marshes, 10 geese on poorly managed salt marshes, and 0 geese on unmanaged salt marshes. The figures used here are more conservative than those obtained by Ebbinge (1992) because most of the unmanaged salt marshes in Northwest Jutland rapidly deteriorate, being abandoned by the geese due to the growth of reed. In contrast, the salt marshes along the more saline Wadden Sea have a much slower succession rate (and hence deterioration rate (Olff et al. 1997), caused partly by the grazing geese).

Results

Danish Wadden Sea

Goose site use

The Wadden Sea was considered an important staging area for the population by Salomonsen (1958), Fog (1967, 1972), and Madsen (1984, 1987), but no regular counts of larger flocks were made before 1986. It has now been confirmed that light-bellied brent geese stage primarily in the northern Danish Wadden Sea (Clausen & Fischer 1994). The number of light-bellied brent geese using the Wadden Sea declined during the 1990s (Clausen et al. 1999), and as a consequence, goose site use declined from 55,000 goose-days in 1986/

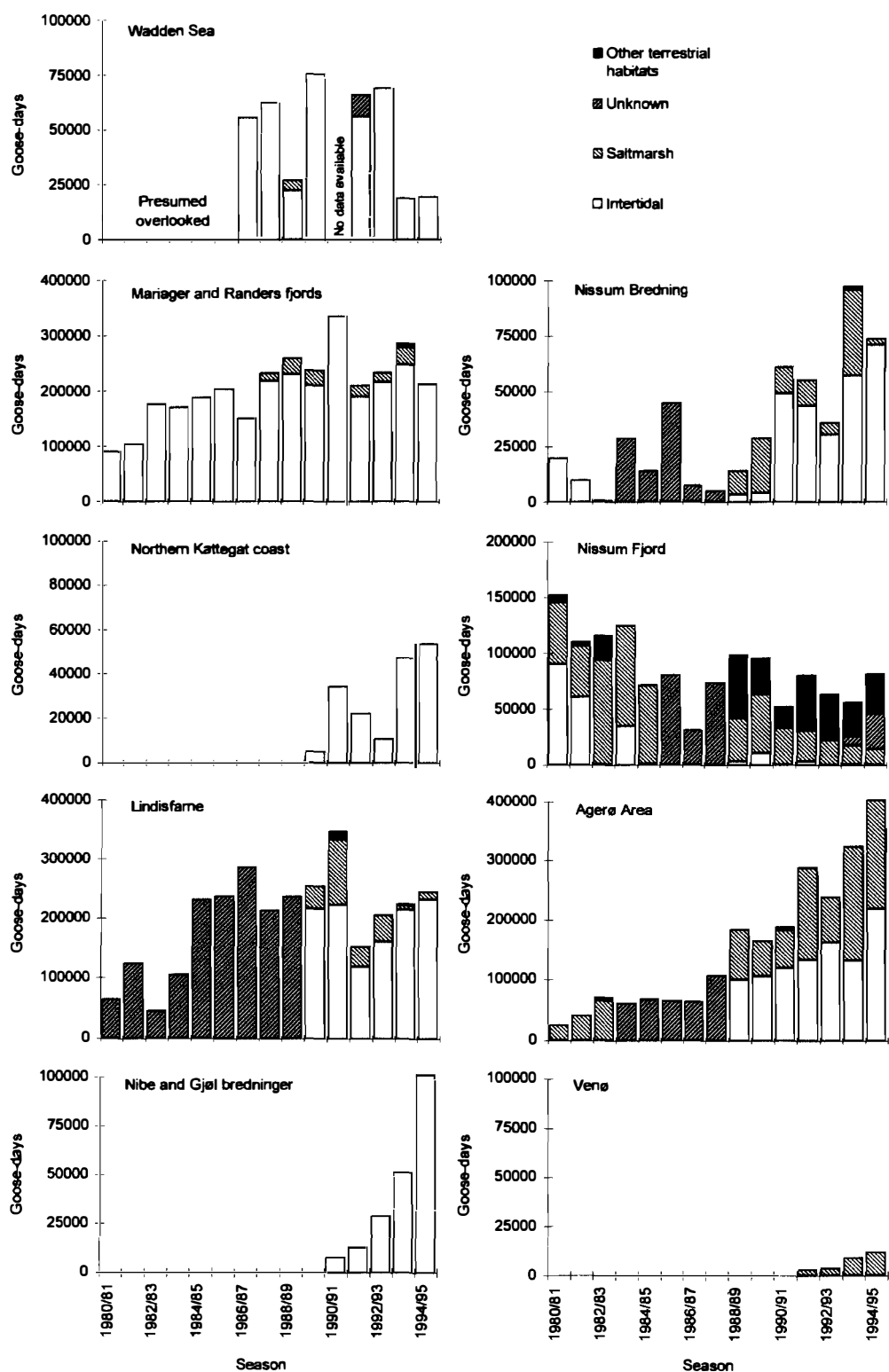
87–1989/90 to 40,800 goose-days in 1991/92–1994/95 (both estimates averages of four seasons) (Fig. 2).

Habitat use and goose distribution

In the Wadden Sea the light-bellied brent geese feed during low tide on intertidal mud flats, where *Z. marina* and *Z. noltii* are the main food items. At high tide the geese fly to high tide roosts where no food is available (Clausen & Fischer 1994). Clausen & Fischer (1994) described how the brent geese in the autumns of 1986 and 1987 only used feeding areas a few kilometres east of the island of Fanø, and all went to roost at Keldsand (Figs. 3 and 4). In autumn 1988 >500 geese were observed along the coast of mainland Jutland as well, and in autumn 1989 more than half of the geese staging in the Wadden Sea used several new feeding areas and high tide roosts, all along the mainland coast (Fig. 3). The new distribution pattern emerging from 1987 to 1989 has been consistent in the 1990s, with approximately half of the birds staging near Fanø and half near Jutland in all the studied years.

Habitat and food availability

Data on changes in food availability in the Danish Wadden Sea are scarce, but very few *Zostera* beds occur in the area (Fig. 4). Furthermore, concurrent data from three important feeding sites for light-bellied brent geese indicate that the densities of food plants in the area are low at present. Thus, low densities of *Zostera* were found during visits to the mud flats of Søjord, Klyngvese Sand, and Råhede in September 1989. At Søjord the leaf cover was estimated to be 15.3% for *Z. marina* and 0.7% for *Z. noltii* (Clausen & Fischer 1994). At Klyngvese Sand it was found that feeding bout lengths *Z. noltii* feeding light-bellied brent geese were comparable with those of dark-bellied brent geese feeding at 10–20% leaf cover of *Z. noltii*, and similar results were found in *Z. marina* feeding light-bellied brent geese at Råhede and Søjord (Table 1). Approximately 40% of the brent geese at Råhede were observed paddling, i.e. trampling in sediment submerged under 5–10 cm of water, thereby loosening whole *Zostera* plants from the sediment. Madsen (1988) showed that this behaviour increased in importance as *Zostera* cover decreased, and a level of 40% brent geese paddling



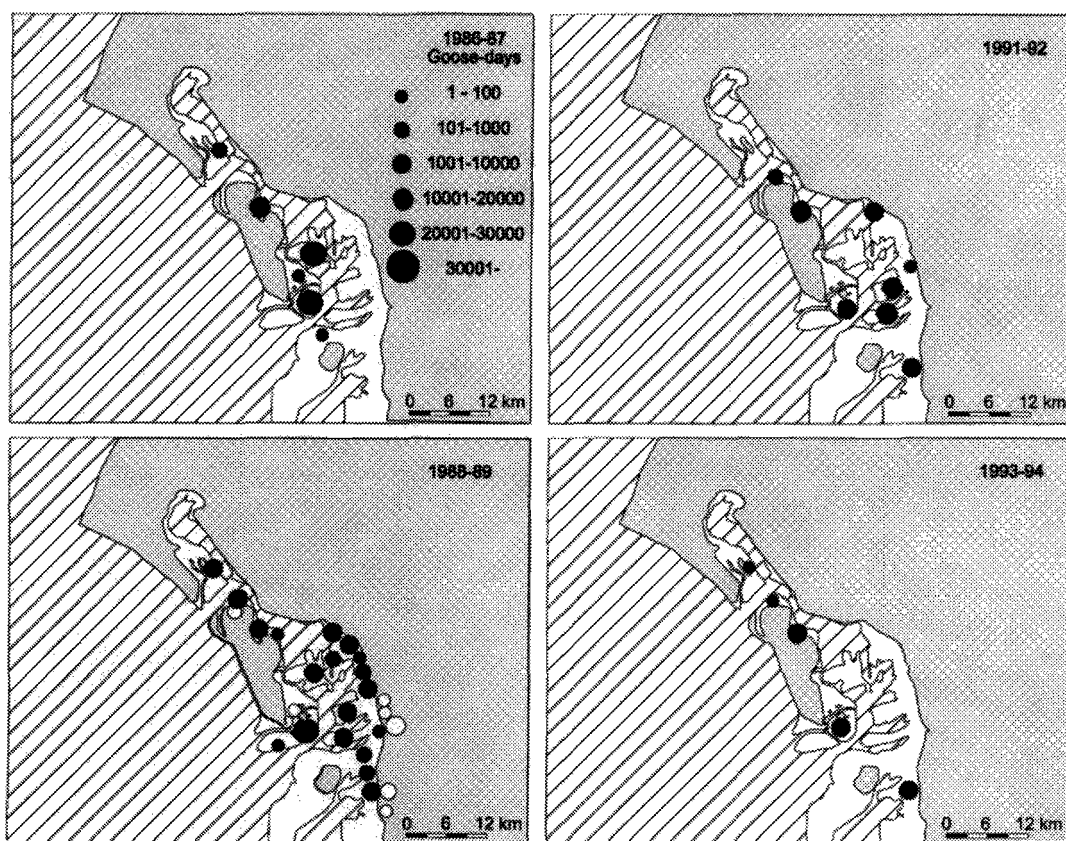


Fig. 3. Distribution of light-bellied brent geese in the Danish Wadden Sea, 1986–1994. The circles indicate numbers of goose-days spent in the period 1 September–31 December (averages for each two-year period); filled circles give flocks feeding/roosting on intertidal mud flats; open circles flocks feeding on salt marshes. For legends concerning different habitat types, and the position of sites mentioned in the text, please see Fig. 4.

in a flock was only observed at very low *Zostera* cover (0–20%).

Discussion

Birds are well known for their ability to search for, find and use patches of abundant food supplies (e.g. Kamil et al. 1987). In agreement with this, Madsen (1988) described how dark-bellied brent geese, when undisturbed, selected those areas where leaf cover of *Z. noltii* was highest. We therefore argue that light-bellied brent geese will feed in the best foraging sites within the parts of the Danish Wadden Sea they normally use. The

feeding performance of light-bellied brent geese in mid-September 1989 in three of the most used sites was comparable to that observed in dark-bellied brent geese feeding on *Z. noltii* at 10–20% of leaf cover (Clausen & Fischer 1994). This suggests that the coverage of the *Zostera* beds was depleted to 10–20% by mid-September. Madsen (1988) recorded 80% coverage in September and depletion to 10–20% coverage in November. Van Eerden (1984) showed that threshold densities in food supplies are found, below which feeding is no longer profitable for the birds. Charman (1979) found a threshold of around 15% leaf coverage for dark-bellied brent geese feeding on *Z. noltii*. Madsen (1988) agreed with this threshold cover

Fig. 2. Development in habitat use expressed as goose-days per season used by the Svalbard light-bellied brent goose population in the nine wintering sites 1980/81–1994/95. Other terrestrial habitats include pastures, cereal fields, grasslands and bait sites.

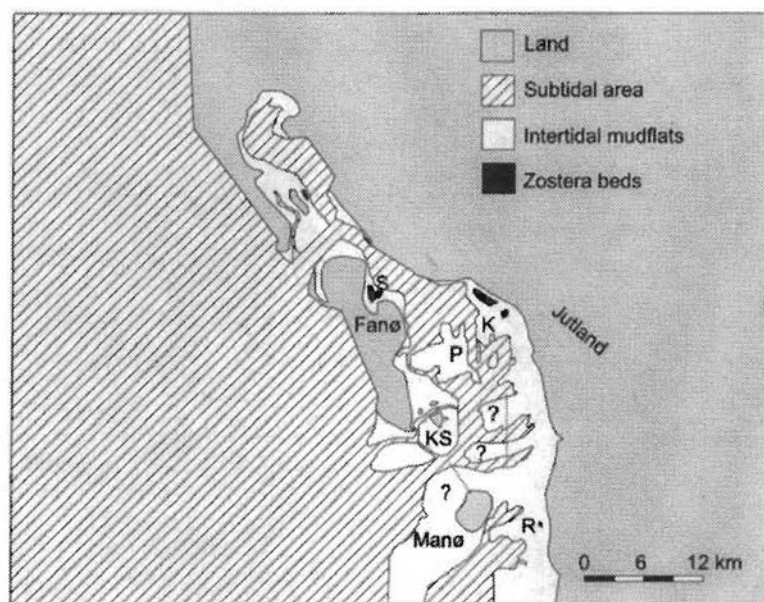


Fig. 4. The distribution of *Zostera* spp. in the northern part of the Danish Wadden Sea, 1988–89. In the black areas the coverage locally exceeded 10–20%. ? denotes unchecked areas; P = Pendersand, an important feeding site for light-bellied brent geese in 1986–87, where *Zostera* occurred formerly but not in 1989; KS = Keldsand, the main high tide roost site until 1989; S = Søjord, K = Klyngvese Sand and R = Råhede, the three important feeding areas in September 1989, where observations on feeding bouts were made (redrawn from Clausen & Fischer 1994).

and argued that the depletion of food supplies to this threshold caused the birds to change habitat or leave the area. Therefore we explain the earlier departure of light-bellied brent geese from the Wadden Sea since the late 1980s by a decrease in food supplies within the staging area. This decrease in food supplies is not caused by exploitative food competition from increasing numbers of the two other important herbivorous waterfowl using the same areas, viz. dark-bellied brent geese and wigeon *Anas penelope*. On the contrary, the dark-bellied brent geese have shown an even more drastic decline in their use of the area, as have the wigeon (Clausen & Fischer 1994). The local declines in use of the area by the

two subspecies of brent geese can not be explained by decreases in their total population sizes (Madsen et al. 1990; Madsen 1992; Clausen et al. 1998). Instead it appears that they were caused by reductions in *Zostera* availability within the area. *Zostera* is disappearing from areas east of Fanø, where it formerly occurred (Fig. 4), and peak densities of *Zostera* biomass in summer have diminished within areas where the plant still is found. Two reasons behind the observed *Zostera* decline may be a recent increase in eutrophication levels in the northern part of the Danish Wadden Sea and deposition of sludge dredged from Esbjerg Harbour in the area east of Fanø (Clausen & Fischer 1994).

Table 1. Length of feeding bouts of light-bellied brent geese feeding on *Zostera* spp. in the Danish Wadden Sea, September 1989 (from Clausen & Fischer 1994). For comparison, corresponding feeding bout lengths are shown for dark-bellied brent geese feeding at 10–20% and 80% coverage of *Zostera noltii*, respectively (from Madsen 1988). *Significantly greater than the feeding bouts measured on light-bellied brent geese in September 1989 (t-test, $P < 0.05$); NS not significantly different from the feeding bouts measured in 1989 (t-test, $P > 0.05$).

Observation site, <i>Zostera</i> species and date	Feeding bout sec Mean \pm SD		Sample size N
Klyngvese Sand, <i>Z. noltii</i> , 13.09.89	11.3 \pm 15.79		35
Råhede Vade, <i>Z. marina</i> , 06.09.89	5.7 \pm 5.24		10
Søjord, <i>Z. marina</i> , 15.09.89	8.5 \pm 6.02		40
10–20% coverage of <i>Z. noltii</i> (Madsen 1988)	9.7 \pm 6.62	NS	32
80% coverage of <i>Z. noltii</i> (Madsen 1988)	36.0 \pm 30.14	*	19

Mariager and Randers fjords

Goose site use

An earlier arrival in autumn and a slight increase in numbers of geese using the area have resulted in an increase in total goose site use, despite the fact that the geese leave the area earlier (Clausen et al. 1998). In the period 1980/81–1982/83, 122,600 goose-days were spent in the area, and in 1992/93–1994/95, 244,000 goose-days (both estimates are averages of three seasons) (Fig. 2).

Habitat use and goose distribution

In Mariager and Randers fjords the brent geese primarily feed on subtidal rooted submerged macrophytes, i.e. *Z. marina* and *Ruppia* spp., and floating thalli of *Ulva lactuca* (Clausen 1994). During 1980–85 the principal feeding areas were restricted to the outermost parts; now they are found some kilometres inside the fjords (Fig. 5). Furthermore, in 1980–85 the geese fed on the subtidal habitats throughout the staging period. In the winter 1987/88 the first flocks of brent geese were observed feeding on salt marshes (Fig. 5), and in 1993/94 flocks were also observed feeding on pastures and winter cereal fields, with an average of 10.3% of goose-days being used on land during 1992/93–1994/95 (Fig. 2).

Habitat and food availability

There is evidence from Mariager Fjord that *Z. marina* stands in the outer end of the fjord disappeared in the 1980s, whereas the status of *Z. marina* in the inner parts of the fjord is more stable (Fig. 6) (Jørgensen 1980; Nordjyllands Amt 1988a; Clausen 1990). Mariager Fjord is the most important of the two fjords for the brent geese and has increased in importance during the 1980s (Fig. 5), and Randers Fjord is now only used in mid- and especially late winter. This is probably explained by the generally low densities of *Ruppia*, *Zostera* and *Ulva* in Randers Fjord at present (Clausen 1990). About half of the salt marshes in the area are poorly managed or unmanaged (Table 2). The sea-grass samples taken in October and November 1993 demonstrated that the food supplies in the main feeding area had been significantly reduced from early October to mid November. The avail-

able *Zostera* biomass declined from 31.1 g/m² to 3.9 g/m², and the biomass in the *Ruppia* dominated community declined from 17.1 g/m² to 12.0 g/m² (Fig. 7). The latter was not significant, but it is worth noting that the samples were taken at a depth of 50 cm. The brent geese can only reach 40 cm below surface when up-ending (Clausen 1994), and *Ruppia* rarely grows to a length of more than 20 cm (P. Clausen, unpubl. data). This suggests that less than half of the 12.0 g/m² in the *Ruppia* community in November should be available to the feeding brent geese.

Discussion

The overall change in foraging areas used by brent geese in Mariager Fjord in the 1980s is probably caused by a decline of *Zostera* in the outermost fjord. The decline is not due to eutrophication. There is no evidence of eutrophication in the outer part of the fjord (Nordjyllands Amt 1988a; Clausen 1990), but some former *Zostera* areas are now covered with silty sediments, less suitable for *Zostera* growth. The establishment of the Overgaard barrage in the early 1960s changed the width of the mouth of the fjord to the sea from 2 km to 400 m (Fig. 5). This caused sand deposition in the outer part of the fjord, and a consequent *Zostera* decline (Århus and Nordjyllands Amt 1998).

The earlier departure of geese from Mariager and Randers fjords in the late 1980s seems to be related to the depletion of food supplies in the fjords. This is indicated by the predominant use of salt marshes as foraging sites by the brent geese late in season. Similar shifts from intertidal to terrestrial habitats have been explained by the depletion of *Zostera* and algae resources by Charman (1979) and Tubbs & Tubbs (1982). In 1989/90 brent geese, coots *Fulica atra* and mute swans *Cygnus olor* all fed in the areas with the highest densities of food plants early in the season, but the coots and mute swans remained longer in these areas. In contrast, although the brent geese initially fed in areas of high food densities, they later switched to forage in areas with very low densities (Clausen 1994). Recent studies in autumns 1992 and 1993 confirmed that *Zostera* supplies are indeed depleted during autumn, and that this may partly be caused by exploitative food competition between brent geese, coots and mute swans (P. Clausen & H. Eittrup unpubl. data). The

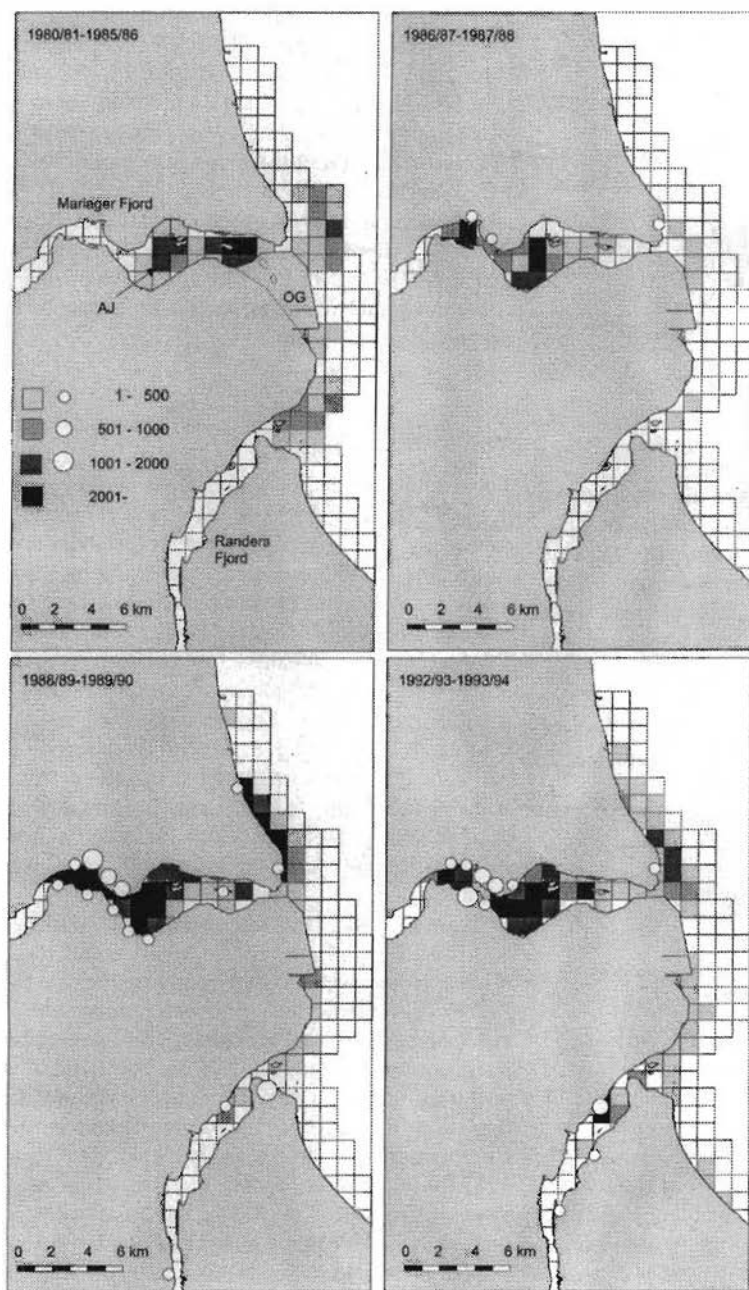


Fig. 5. The distribution of light-bellied brent geese in Mariager and Randers fjords, 1980–94. Feeding sites on the fjord are given in a $1 \times 1 \text{ km}^2$ grid, on land as open circles, respectively. The importance of different feeding areas is given as an index (the sum of all observed flocks). On the fjord areas an area correction was applied to incomplete quadrats (Jørgensen et al. 1994). AJ is Ajstrup Bugt, where *Zostera* and *Ruppia* samples were taken; OG indicates the Overgaard barrage, and the stippled lines the former coastline and two islets.

brent geese are the first affected by this competition because the food resources are first depleted for the brent geese. This is because coots and mute swans can feed at greater depths than brent geese, the first by diving and the latter by use of their

longer necks. The interpretation is that to avoid competition, the brent geese disperse to fjord areas with low densities of food, alternatively switch to salt marshes, or ultimately leave the area. In conclusion, it appears that the carrying capacity

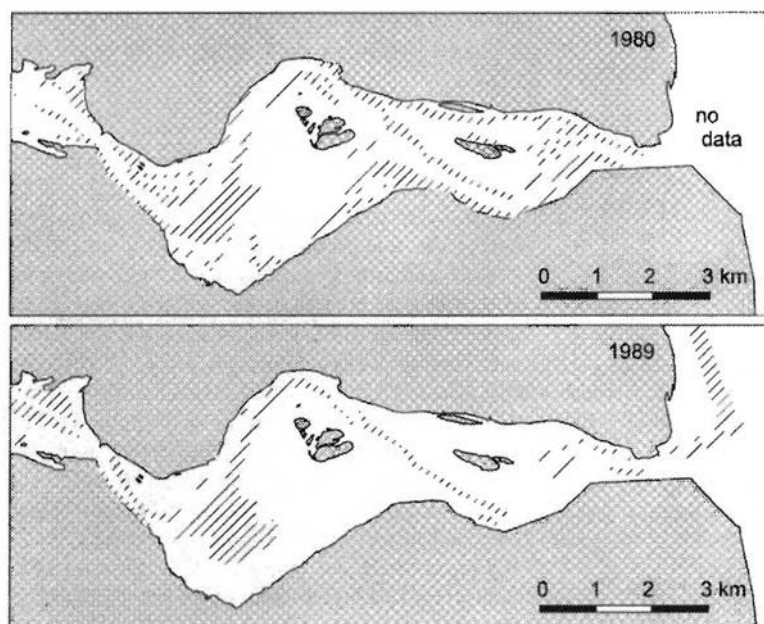


Fig. 6. The overall distribution of *Zostera marina* in the outermost end of Mariager Fjord, 1980 and 1989 (based on Jørgensen 1980; Clausen 1990).

Table 2. Areas of submerged/intertidal *Zostera*, *Ruppia*, green algae *Ulva/Enteromorpha* beds and salt marshes within the nine staging areas of international importance used by light-bellied brent geese in 1980–95. *Zostera*, *Ruppia*, and algae data are summarised from Limfjordskomiteén (1987); Clausen (1990); Limfjordsovervågningen (1992); Clausen & Fischer (1994); Ringkjøbing Amt (1994–97); Percival et al. (1996); Clausen et al. (1996); Madsen (1998a); B. Laubek (pers. comm.). + in *Zostera/Ruppia* scores indicates presence of these habitats, but the exact area unknown or negligible. The area and management status of salt marshes (based on own data, except Northern Kattegat coast and Nibe and Gjørl bredninger, based on Nordjyllands Amt (1988b, 1991)), and their estimated carrying capacity and present use by brent geese for the sites used in spring is tabulated. The salt-marsh area in the Wadden Sea was not calculated, due to the insignificant use of salt marshes in this area (Clausen & Fischer 1994).

Area	<i>Zostera</i> km ²	<i>Ruppia</i> km ²	Green algae km ²	Salt marsh km ²	Salt-marsh management status			Estimated carrying capacity spring geese	Peak count spring 1995 geese
					Well managed %	Poorly managed %	Unmanaged %		
Danish Wadden Sea	5.0	0.0	+	+					
Mariager and Randers fjords	4.3	4.8	1.3	4.2	49.6	13.8	36.6		
Nibe and Gjørl bredninger	45.0	+	+	5.3	≈48.0	≈33.0	≈9.0		
Northern Kattegat coast	+	+	+	4.2	≈30.0	≈20.0	≈50.0		
Lindisfarne	7.7	–	+	0.4	0.0	0.0	100.0		
Nissum Bredning	4.5	+	+	0.9	91.3	0.0	8.7	2,500	325
Nissum Fjord	0.0	+	+	2.2	29.1	0.8	70.0	1,900	1,020
Agerø area	11.3	–	–	7.5	81.4	7.5	11.1	19,000	3,500
Venø	1.0	–	+	0.3	40.0	60.0	0.0	575	200

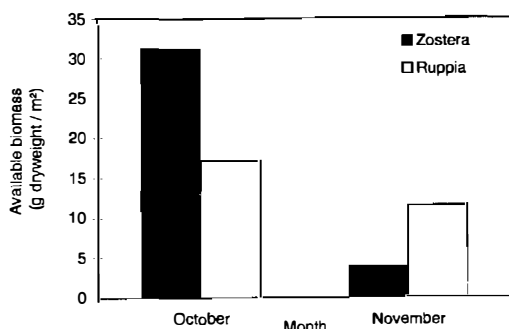


Fig. 7. Development in available biomass of *Zostera marina* and total biomass of seagrasses in the *Ruppia* dominated community (biomass of *Ruppia* spp., *Chara* spp. and *Z. marina* pooled) from early October to mid-November 1993. The decline in available *Zostera* biomass is modelled from a highly significant decline in average leaf lengths (53.5 cm in October, 33.4 cm in November; $t = 5.33$, $df = 109$, $P < 0.0001$; Welch's approximate t-test for samples with unequal variances), and a decline, though not significant, in *Zostera* biomass (151.1 g/m² in October, 65.7 g/m² in November; $t = 2.96$, $df = 3$, $P = 0.059$; Welch's approximate t-test for samples with unequal variances). The decline in biomass in the *Ruppia* community is not significant ($t = 1.62$, $df = 22$, $P = 0.12$, Student's t-test).

for brent geese of the subtidal habitats within Mariager and Randers fjords has been reached.

Lindisfarne

Goose site use

As with Mariager and Randers fjords, the earlier arrival in autumn and increase in brent geese numbers caused an increase in total goose site use, despite an earlier departure of geese from the area. In 1980/81–1982/83, 77,200 goose-days were spent in the area, and in 1992/93–1994/95, 224,400 goose-days (both estimates are averages of three seasons) (Fig. 2). Included in the estimate for the 1990s are goose-days spent by dark-bellied brent geese. In 1973–88 very few dark-bellied brent geese were seen among the light-bellied brent geese, with annual peak counts ranging from 5 to 39 geese (NCC counts, D. O'Connor unpubl. data), but during 1989–95 annual peaks ranged from 280 to 453 geese. The presented number of goose-days spent by brent geese at Lindisfarne in

the 1990s thus includes 12.9% (average, range 9.8 to 20.5%) spent by dark-bellied brent geese per season.

Habitat use and goose distribution

In Lindisfarne, the light-bellied brent geese feed during low tide on intertidal *Zostera angustifolia*, *Z. noltii* and *Enteromorpha* beds. At high tide most birds roost on mud flats, but small groups fly to feed at salt marshes. Distributions of brent geese and wigeon were mapped in 1973–74 (Fig. 8) (Boorman & Ranwell 1977), when brent geese and wigeon to a major extent used discrete feeding areas, with the majority of brent geese feeding on Holy Islands Sands, and the wigeon feeding on Fenham Flats (Fig. 8). In 1989–92, brent geese had switched to feeding on *Zostera* on Fenham Flats, and brent geese and wigeon fed on *Zostera* in the same areas to a higher extent than previously (Fig. 8).

Habitat and food availability

The distribution of *Zostera* was also mapped in 1973–74 (Phil Smith, unpubl. data) (Fig. 8). A comparison of these records with the situation in 1989–92 (Fig. 8) reveals that almost all *Zostera* on Holy Islands Sands disappeared, resulting in a 20% decrease in *Zostera* area from 9.5 to 7.6 km². Studies of food availability during 1989–92 found that *Zostera* and *Enteromorpha* supplies were significantly reduced in the course of the winter, from 21.1 g/m² in September to 5.6 g/m² in February (Fig. 9). Consequently the feeding performance in terms of pace rate and dropping rate declined during winter (Fig. 9).

Discussion

At Lindisfarne there is only minor evidence of eutrophication, and the main reason behind the decline of *Zostera* on Holy Islands Sands is believed to be the establishment of the Holy Island causeway in 1958 (Fig. 8). The causeway led to changes in sedimentation processes and caused a change from muddy to sandy substrate on Holy Islands Sands. The seasonal declines in *Zostera* biomass, pace rate and dropping rate measurements are all comparable to those found by Madsen (1988). This shows that the *Zostera*

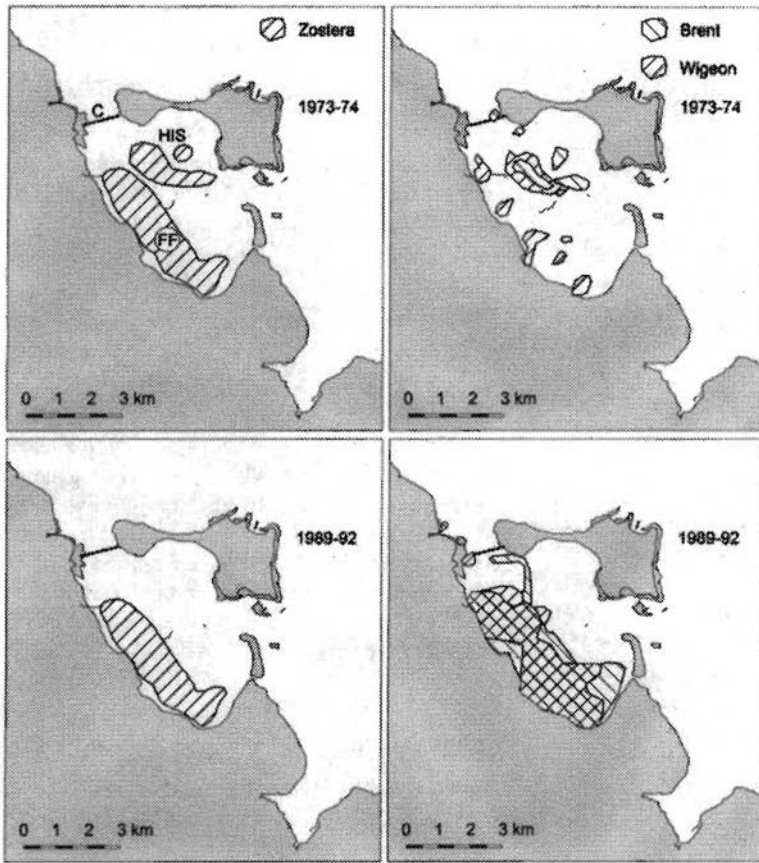


Fig. 8. The overall distribution of *Zostera* spp., and feeding areas for light-bellied brent geese and wigeon at Lindisfarne in 1973–74 (above) and 1989–92 (below). HIS = Holy Islands Sands, FF = Fenham Flats, C = the Causeway (based on Boorman & Ranwell 1977; Phil Smith, unpubl. data).

supplies in February are depleted to threshold levels. Percival et al. (1996) concluded likewise, by using a modelling approach, that *Zostera* supplies became depleted by February. It would be predicted that the brent geese would leave the area or switch habitats (Madsen 1988), which indeed they do by migrating still earlier to the spring staging areas in Denmark in the 1990s.

The recent increase in use of Lindisfarne by dark-bellied brent geese may be seen as an effect of the steady increase of their numbers in Great Britain, particularly at the sites nearest to Lindisfarne, i.e. the Wash and the North Norfolk coast (Owen et al. 1986; Kirby & Cranswick 1993). A continued increase in the numbers of dark-bellied brent geese may lead to increased competition for food supplies between the two subspecies of brent geese and wigeon.

Nibe and Gjøøl bredninger and the Northern Kattegat coast

Goose site use

Very few light-bellied brent geese were observed in these two areas before 1989 (Clausen et al. 1998; Madsen 1998b). Since the winter of 1989/90, flocks of more than 100 light-bellied brent geese were observed annually, with a seasonal maxima of up to 600 birds along the Northern Kattegat coast and 1,100 birds in Nibe and Gjøøl bredninger in the mid 1990s (Clausen et al. 1999). During 1989/90–1991/92, flocks of >200 birds only occurred in these areas from November through January, while in 1992/93–1994/95 both areas were used by >200 birds from September

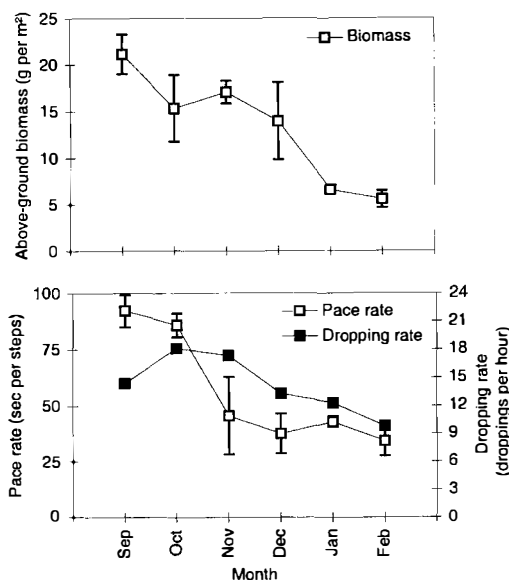


Fig. 9. Development in biomass of *Zostera* in plots where dropping and pace rates were measured on feeding flocks of brent geese (above), and in pace and dropping rates (below), Lindsfærne 1989–92. The significant declines in biomass and pace rates are presented as average values \pm 95% confidence limits (vertical bars). Measurements of dropping rates suggest a decline too ($Z = 1.43$, $P = 0.0771$, method Bédard & Gauthier 1986, excluding September only one data point).

through to March, or even April (Nibe and Gjølbredninger), but numbers still peaked from November through January. According to these observations, total goose site use increased from virtually zero use of both areas in the 1980s to 37,200 goose-days along the Northern Kattegat coast and 60,400 goose-days in Nibe and Gjølbredninger in 1992/93–1994/95 (average of three seasons) (Fig. 2).

Habitat use and goose distribution

In both areas the brent geese primarily feed on *Z. marina* beds (Madsen 1998b; B. Laubek, pers. comm.), but also on *Ruppia* beds and salt marshes along the Northern Kattegat coast (B. Laubek, pers. comm.).

Habitat and food availability

Because of its two large *Z. marina* beds, Nibe & Gjølbredninger is the single most important site for this submerged plant in Denmark, and it would

appear that there should be plentiful space for feeding brent geese. Although *Zostera* densities in the area have declined during the 1990s, partly being replaced by *Ruppia* beds (Madsen 1998b), this has so far had no effect on the numbers of brent geese using the area. The accurate size and status of the *Zostera* and *Ruppia* beds along the Northern Kattegat coast are currently unknown.

Discussion

The recent use of Nibe and Gjølbredninger and the northern Kattegat coast (as well as Nissum Bredning and the Agerø area, see below) in late autumn and winter may be seen as a choice made by many of the geese which formerly staged in Mariager and Randers fjords. By moving away instead of switching to local salt marshes, the geese can continue to feed on submerged *Zostera*, as they do in the four areas mentioned, and thereby probably derive more efficient net energetic gains (cf. Drent et al. 1978/79).

Nissum Bredning

Goose site use

In 1980–87 brent geese only used the area in late winter, i.e. February and March. In the relatively mild winters from 1988/89 to 1994/95, light-bellied brent geese arrived still earlier at Nissum Bredning each year, and a few hundred geese were found throughout November to May. Numbers still peaked in February–March, but large flocks tended to stay longer than previously in the area. As a consequence, the number of goose-days spent in the area increased from 9,900 in 1980/81–1982/83 to 70,500 in 1992/93–1994/95 (both figures are averages of three seasons).

Habitat use and goose distribution

In Nissum Bredning the light-bellied brent geese only fed on *Zostera marina* beds in Limfjorden in the early 1980s (Figs. 2 and 10) (Madsen 1986). Since the late 1980s birds have frequently been observed feeding on salt marshes. Especially during 1993/94 and 1994/95 large flocks were also observed feeding on the *Ruppia*-dominated sea-grass beds in the brackish lagoons Harboør



Fig. 10. The overall distribution of feeding flocks of light-bellied brent geese in Nissum Bredning, 1980/81–1982/83 (redrawn from Madsen 1986) and in 1993/94–1994/95 (expressed as average number of goose-days for the two seasons for each count area). The *Zostera* feeding brent geese is presented in a $1 \times 1 \text{ km}^2$ grid on Limfjorden, salt-marsh feeding brent geese as closed circles, and the total use of each of the three brackish lagoons is indicated in the lagoons (HF = Harboør Fjord; TF = Thyborøn Fjord; AF = Agger Fjord).

Fjord and Thyborøn Fjord on Harboør Tange, and the lagoon on Agger Tange (Fig. 10), making a total of 37.3% of all goose-days spent in Nissum Bredning in 1993/94–1994/95.

Habitat and food availability

The 4.5 km^2 *Zostera* bed in Limfjorden has not changed in overall distribution from 1985 to 1994 (Limfjordskomitéen 1987; Clausen et al. 1996). Most of the salt marshes in the area still have a short sward and are classified as well managed (Table 2), despite the fact that grazing has discontinued in several of these.

Discussion

The distribution and habitat use of the geese in

Nissum Bredning are highly variable from year to year (Fig. 2) (Clausen et al. 1996). This is explained by variations in water level in Limfjorden when the birds use the area. During normal water level conditions, most birds fed on *Zostera* beds in Limfjorden, while they switched to feeding on salt marshes during periods with wind induced high water levels. This situation was dominating during the staging periods in 1989/90 and 1993/94, resulting in particularly high use of salt marshes during these two seasons (Fig. 2). The recent use of the coastal lagoons may reflect the earlier arrival of the brent geese in autumn because the *Ruppia* and *Potamogeton* sea grasses growing there are still available at this time of the year. When the brent geese arrived in February and March in the early 1980s, it is unlikely that any above-ground parts of *Ruppia* and *Potamogeton* would have been available (cf. Kiørboe 1980).

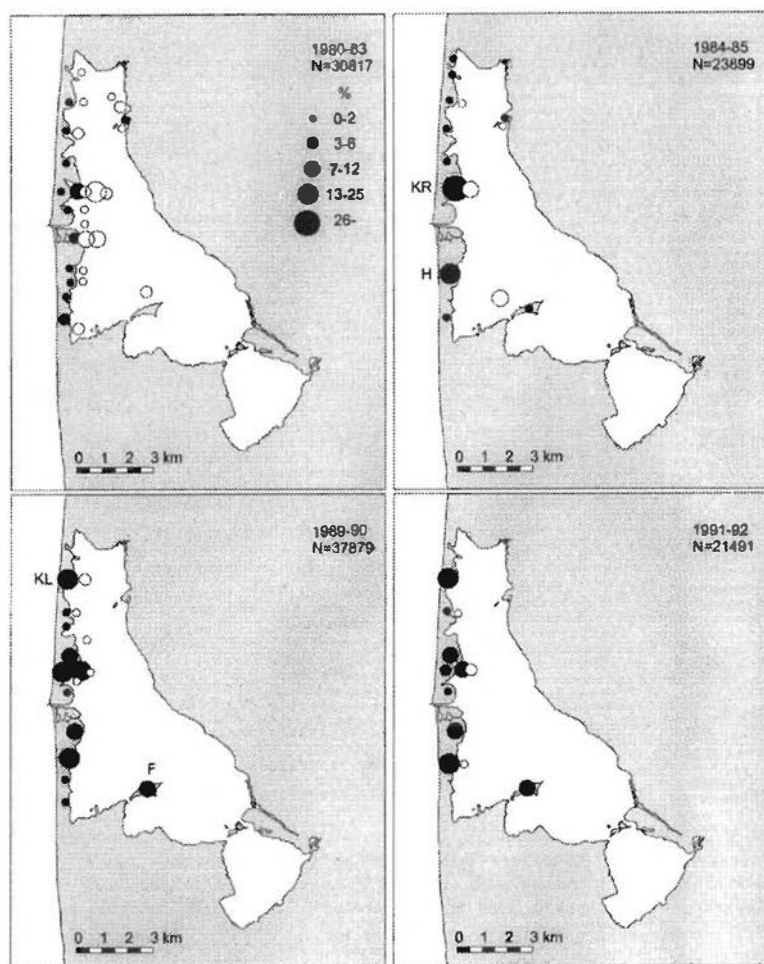


Fig. 11. The distribution of feeding flocks of light-bellied brent geese in Nissum Fjord, 1980–92. The circles give the percentage distribution of all individuals recorded (=N) in the period January–May (pooled data for each period, first map covering four years, the rest two years); closed circles = feeding on land; open circles = on the fjord; KR = Kromanden; H = Holmen; KL = Klægodde (bait site); and F = Fjandø.

Nissum Fjord

1992/93–1994/95 (both figures are averages of three seasons) (Fig. 2).

Goose site use

The site was described by Salomonsen (1957) as an important area for light-bellied brent geese, and several authors have dealt with the use of the fjord by brent geese since then (Fog 1967, 1972; Jepsen 1967, 1984; Madsen 1984, 1986; Christensen 1987). Throughout the 1960s, it was believed that the entire population was found there in spring (Fog 1972, 1979). Since the early 1980s, the number of brent geese staging in the area has decreased to a present level of ca. 1,000 geese in spring (Clausen et al. 1998). As a consequence goose site use has decreased from 125,500 goose-days in 1980/81–1982/83 to 66,700 goose-days in

Habitat use and goose distribution

Formerly, the brent geese fed primarily on submerged *Z. marina* in the fjord throughout spring, only using the salt marshes occasionally during high water levels (Salomonsen 1957; Jepsen 1967). During the early and mid 1980s, the geese switched to feeding primarily on salt marshes (Fig. 2), especially on Holmen and Kromanden (Fig. 11), and pastures were also used (Madsen 1984, 1986; Christensen 1987) (Fig. 2). Two sites, Klægodde and Fjandø, almost unused by the brent geese in 1984–85, became increasingly important as feeding areas in 1989–92 (Fig. 11) and the most

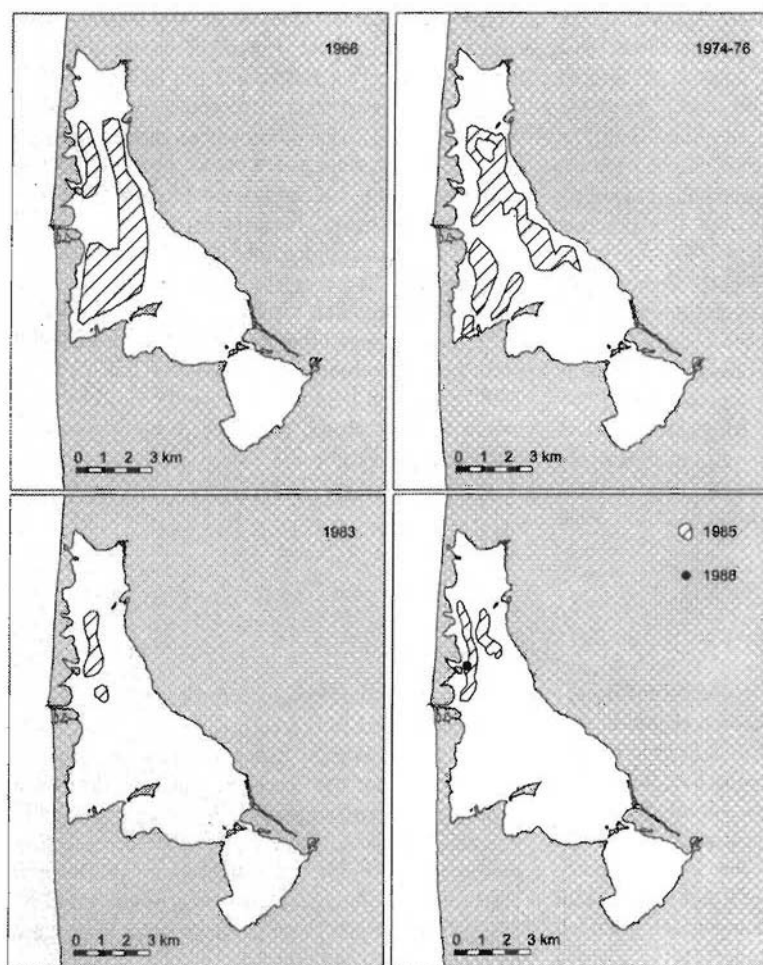


Fig. 12. The overall distribution of *Zostera marina* in Nisum Fjord, 1966–1988. In 1988 a single shoot was found at the site depicted by a dot (based on Jepsen 1967, 1984; Rasmussen 1976; Ringkjøbing Amt 1985a, 1988).

important sites for the brent geese in 1994–95. The attraction on Klægodde is a bait site established in 1989 where pink-footed geese *Anser brachyrhynchus* are baited with barley *Hordeum vulgare* grains on a pasture from mid April to early May. The light-bellied brent geese began using this site immediately and also used newly sown barley fields more frequently than before (Fig. 2). The island of Fjandø consists of low sand dunes, with only a small part of the vegetation being salt marsh, the rest being typical sand dune swards which is unusual habitat for brent geese.

Habitat and food availability

A drastic decline in the distribution of *Z. marina*

occurred during the 1980s, from 11 km² in 1966–76 to zero in 1988 (Fig. 12). There has been some recovery of *Z. marina* during the 1990s (Ringkjøbing Amt 1994–97). The reestablished *Zostera* bed as well as other submerged plants and algae, however, grew at very low densities during the summers of 1990–1994, with average bottom covers (all species pooled) ranging from 10–15%. A new decline in the *Zostera* bed size from 3.0 km² to virtually zero occurred again from 1994 to 1995 (Ringkjøbing Amt 1993, 1994–97). In addition to the loss of *Zostera* habitat, almost half (46%) of the salt-marsh area along the western coast of Nisum Fjord was reclaimed for agriculture in the 1960s and 1970s, thereby effectively reducing the salt-marsh area from 4.1 km² in 1958 to 2.2 km² in 1981 (measured from 1 : 25,000 maps

from the Geodaetical Institute, Copenhagen). Jepsen (1967, pers. comm.) only recorded two minor reclamations in 1965, and no additional reclamations were made from 1981 to 1992 (comparing the 1981 map and own field data), so almost all reclamations were made from 1966 to 1980. The salt marshes were intensively grazed by cattle or hay cut in the 1960s, but this practice ceased in several areas in the late 1970s and early 1980s (Jepsen 1984; Madsen 1984). The marshes are currently growing tall vegetation with the development of reed beds (Jepsen 1984; Christensen 1987). From 1985 to 1992, only minor changes in management practice occurred, comparing our 1992 data with those of Ringkjøbing Amt (1985b). Only 30% of the salt marshes are managed today, and the carrying capacity for spring fattening geese was estimated at ca. 1900 geese (Table 2).

Discussion

The overall decline of *Zostera* in the fjord (Fig. 12) was caused by severe eutrophication (Ringkjøbing Amt 1985a, 1988). The species disappeared almost totally during 1988 when the North Sea sluice was closed for repair during a few months, and the salinity in the fjord as a consequence fell below 6–8‰, which is considered the lower salinity tolerance limit for *Z. marina* (Ringkjøbing Amt 1993). The same sluice management induced reduction in salinity occurred in 1995, when a new disappearance of *Zostera* was recorded. Since 1976 the decline in *Zostera* has gradually reduced the foraging opportunities for brent geese in the area. Reclamation of salt marshes for agricultural use, and the cessation of both cattle grazing and mowing of other salt marshes in the late 1960s and 1970s, have further reduced foraging opportunities. Although the data collected at Nissum Fjord cannot be analysed statistically (because most mappings of *Zostera* and salt marsh availability were made in years without simultaneous goose studies), it is obvious that the salt marsh reclamations per se did not affect the brent geese in the 1960s and 1970s. The brent geese continued to feed on *Zostera* until the early 1980s (Figs. 2 and 11), and it was only after the decline of *Zostera* that salt-marsh feeding became important (Fig. 11). Salt-marsh feeding probably declined in the late 1980s because of poor salt-marsh management. This has prompted some brent geese to

forage on pastures, sand dunes and newly sown cereal fields in spring (Fig. 2). The recent use of newly sown cereal fields and the bait site could reflect a high energetic profitability of these sites (Madsen 1985). Some brent geese decided to leave the area and search for new foraging areas, resulting in the successful establishment of the Agerø spring haunt. In spite of the reduction of quality of Nissum Fjord habitats for spring staging brent geese, the carrying capacity of the salt marshes exceeds that used by the geese (Table 2); but it must be noted that the peak number of 2,700 brent geese recorded in spring 1976 (Clausen et al. 1998) could not be maintained in the fjord by salt-marsh feeding alone, given the present management practice (Table 2).

Agerø area

Goose site use

In spring 1973 the first small flocks of light-bellied brent geese were observed feeding on salt marshes on the island Agerø. Since then the number of brent geese in the area has increased almost annually to approximately 3,500 geese in 1994–95, and the geese have prolonged their staging period from March through May in 1980–83 to November through May at present (Clausen et al. 1998). The number of goose-days spent in the area increased from 45,000 in 1980/81–1982/83 to 322,600 in 1992/93–1994/95 (both figures are averages of three seasons).

Habitat use and goose distribution

In 1980–83 brent geese only fed on salt marshes on Agerø (Madsen 1984, 1986). In 1988–95, 29% (range 5–48%) of goose-days in spring were spent on *Zostera* beds, 1% (range 0–4%) on spring barley fields, and the remaining 67% (range 48–74%) on salt marshes. During autumn and winter in 1988–95, *Zostera* beds were the primary feeding habitat with 92% (range 51–100%) of the goose-days being used there. On an annual basis these figures give an almost even use of salt marshes and *Zostera* beds in recent years (Fig. 2). Until the mid-1980s, brent geese were confined to areas in the immediate vicinity of Agerø, but since then more remote salt marshes and *Zostera* beds have

been used, the most recent being 12 km away from Agerø (Jørgensen et al. 1994).

Habitat and food availability

From 1988 to 1992, densities of *Zostera* increased considerably and new areas were colonised by *Zostera* around Agerø (Drachmann et al. 1993) (Fig. 13). Inside the 12 km range used by the geese, 7.5 km² of salt marshes are found. The majority are well managed, most of them grazed by cattle, and their carrying capacity was estimated at ca. 19,000 geese in 1992 (Table 2).

Discussion

The large use of *Zostera* in recent years is seemingly not related to the limitation of resources found on the salt marshes, at least not in 1989 and 1993, when the brent geese only grazed 31% and 20%, respectively, of the net above-ground primary production of *Puccinellia maritima* during April–May in an experimental plot (Clausen 1998, this volume). There are indications of a positive development in *Zostera* stands throughout most of Limfjorden in the late 1980s and early 1990s, especially around Agerø (Limfjordsovervågningen 1992; Drachmann et al. 1993). Three factors or a combination of these may have caused this development (reviewed in Drachmann et al. 1993): (1) Large investments in waste water cleaning plants in the 1970s and 1980s have led to a reduction in the eutrophication of Limfjorden; (2) a series of extraordinary mild winters 1987–92 have allowed the *Zostera* to grow throughout the year and there have been no die backs due to bottom freezing in mid-winter; and (3) the prohibition of blue mussel *Mytilus edulis* fishery around Agerø in 1987 stopped the negative impact which the fishery was believed to have had on *Zostera* growth in Limfjorden. Whichever factor led to the reestablishment of *Zostera* in Limfjorden, the historical literature (Salomonsen 1957; Jepsen 1967) and the present habitat use of brent geese around Agerø suggest that the 'optimal' spring feeding strategy for the light-bellied brent geese is to combine the two habitats, *Zostera* beds and salt marshes. This is because the brent geese feed on the *Zostera* beds at low water levels and switch to salt marshes during high water levels (Clausen 1994). The use of the *Zostera* gives the geese higher energetical intake than feeding on

the salt marshes, but the salt marshes acts as an important alternative feeding habitat, when *Zostera* is unavailable during high water levels (Clausen 1994). Only two of the four areas used at present in spring by the light-bellied brent geese offer optimal conditions, i.e. Nissum Bredning and especially the area around Agerø, where large areas of well-managed salt marshes and large *Zostera* beds are found (Table 2). In this connection it is worth noting that the sudden increase in the numbers of light-bellied brent geese using the Agerø area from 1987 to 1992 (Clausen et al. 1998) coincided with the extinction of *Zostera* in Nissum Fjord (Fig. 12), and the increase in densities of *Zostera* around Agerø (Fig. 13).

Venø

Goose site use

In spring 1991 the first small flocks of light-bellied brent geese were observed feeding on salt marshes on the island Venø. Since then the number of brent geese using the area has increased annually to a maximum of 200 geese in spring 1995. The staging period is from March through May, with a slightly earlier arrival in recent years. This leads to an increase in the number of goose-days from zero in 1990 to 12,000 in 1994/95.

Habitat use and goose distribution

The brent geese have only been observed feeding on salt marshes, despite the presence of *Zostera* beds in the adjacent Limfjorden (Table 2).

Habitat and food availability

The salt marshes in the area are grazed. This activity was resumed recently (warden A. Ulfkjær, pers. comm.), and it is expected to result in improved management (i.e. larger well grazed area) in future years.

Discussion

The establishment of this staging area may be a result of the continual flow of individuals away from Nissum Fjord (Clausen et al. 1998). Alter-

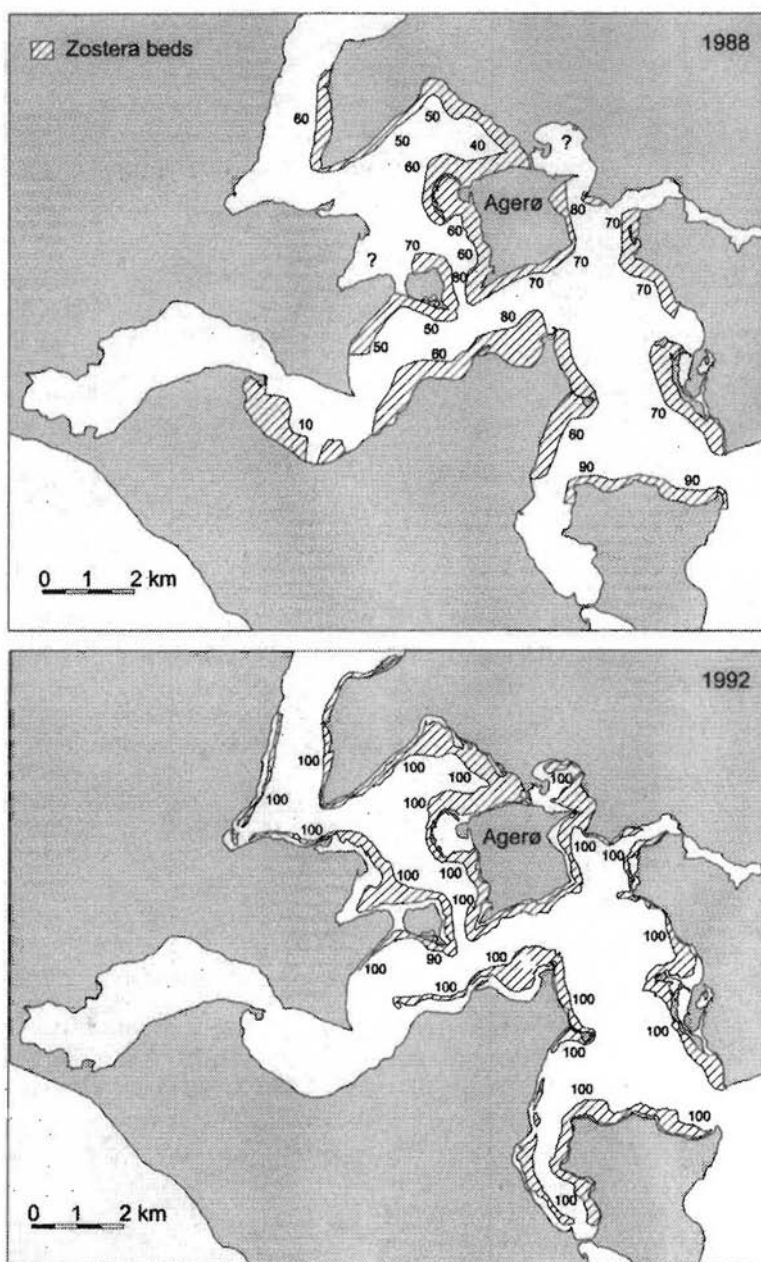


Fig. 13. The overall distribution and bottom covers of *Zostera marina* around Agerø, 1988 and 1992. The hatched areas give the distribution and the figures denote maximum bottom covers of *Zostera* in specific areas? denotes two areas where some *Zostera* beds probably were overlooked in the 1988 survey; the map for 1992 was drawn from aerial photographs with support from a field survey, whereas the 1988 map only is based on field survey, hence the 1992 mapping is considered more accurate (based on Limfjordskomitéen 1989; Drachmann et al. 1993).

natively, the site may have been colonised by birds from Agerø, which, as mentioned earlier, have been flying in recent years to more distant feeding sites away from the roost site at Agerø. Birds within a range of 12 km away from Agerø are known to roost communally at Agerø, while the birds at Venø (16 km away) roost at Venø.

Discussion

The 'domino effect' of changing *Zostera* supplies

The observed changes in site use by the light-

bellied brent goose population can be interpreted as a response to changes in availability of their preferred food resource—*Zostera*. It is evident that *Zostera* beds have decreased in extent or even totally disappeared at all staging areas where overall goose site use (expressed in goose-days) has declined or levelled off. The immediate response of the brent geese to a decreasing *Zostera* resource in their traditional staging areas was to switch to other *Zostera* beds in the immediate surroundings (or to alternative intertidal/submerged food supplies, such as *Ruppia*, *Potamogeton*, *Ulva*, *Enteromorpha*), a response observed in the Danish Wadden Sea, Mariager Fjord, and at Lindisfarne. In Nisum Fjord, where the *Zostera* beds disappeared, the only option was to switch to alternative feeding habitats, or abandon the area completely. With the increase in population size, the total number of goose-days spent on the wintering areas have gone up from ca. 500,000 goose-days per season in the early 1970s (population ca. 2,000 birds, staging in the wintering areas from mid September to last week of May) to ca. 1,300,000 goose-days in the mid 1990s (population ca. 5,000 birds). This additional goose exploitation can be supported on the traditional staging areas, where suitable habitats within these have the potential to do so. The data presented on feeding performance and/or *Zostera*, *Ruppia*, *Enteromorpha* food densities from the Danish Wadden Sea, Mariager and Randers fjords, and Lindisfarne strongly suggest that the carrying capacities of the remaining intertidal and submerged food supplies have been reached. As a consequence, the geese are faced with the decision either to leave the sites or switch to terrestrial habitats (cf. Madsen 1988). Adoption of the first option is demonstrated by the earlier departure from all three sites (see Clausen et al. 1998 for details), while the latter option has only been observed at Mariager and Randers fjords and Lindisfarne. The number of birds that have switched to terrestrial feeding is, however, few compared to the numbers that could continue to feed on *Zostera* or other intertidal food resources by colonising new sites. Expressed in numbers, 40,500 goose-days were spent on terrestrial habitats at Lindisfarne and Mariager and Randers fjords and 235,000 goose-days on *Zostera* beds in Nibe and Gjølbredning, the Northern Kattegat coast, and the Agerø area in 1992/93–1994/95 (average of three seasons, only including the period September–mid-March, the period when

the geese stage at Lindisfarne, Mariager and Randers fjords; this study).

Why stay with *Zostera*?

There are several good reasons why the brent geese should feed on *Zostera* if possible (see Clausen 1994, 1998 for details): (1) by feeding on *Zostera* in autumn they utilise the energetically most favourable food resource among those available in the near coastal zone (Drent et al. 1978/79); (2) the same applies to the spring fattening period, when intake rates and metabolisable energy contents of *Zostera* are similar or higher than when the geese feed on salt-marsh halophytes (Clausen 1994); (3) the geese fly less, and thereby save energy, when feeding on *Zostera* compared to salt marshes (Clausen 1994); and (4) *Zostera* productivity is higher than that of salt-marsh halophytes (Clausen 1998). Thus *Zostera* may be considered as a superior food choice for brent geese. This does not mean that brent geese are dependent on *Zostera*, but the points above strongly suggest that they perform better when fed on *Zostera* (in terms of autumn fattening—which may reduce winter mortality, and spring fattening—which may influence subsequent breeding success).

Proposals for future management

Zostera beds disappeared from most Danish waters when the 'wasting disease' almost wiped out *Z. marina* in the Atlantic region in the 1930s (Rasmussen 1977). There has been some recovery since then, but the present distribution of the plant still falls far short of the previous distribution (Olesen 1993). This is most likely due to the rather heavy influence of eutrophication in Danish waters, that has a negative impact upon *Zostera marina* growth (Borum et al. 1990; Sand-Jensen & Borum 1991). In 1987, Denmark implemented the national Action Plan for the Aquatic Environment, aimed at improving water quality in streams, lakes and coastal waters. There is an expectation that recovery of *Zostera marina* beds will occur in due time, but so far the results are not convincing (Jensen et al. 1997). Experiments to transplant *Z. marina* to areas where it previously grew have been made, with varying success (Christensen et

al. 1995). Hence, it is unlikely that large areas of *Z. marina* will re-establish itself in the near future.

When *Zostera* becomes unavailable either due to depletion or inaccessible due to high water levels, salt marshes act as an important alternative feeding habitat (Clausen 1994, 1998). Most of the sites the light-bellied brent geese use in Denmark have quite substantial areas of salt marshes, several of which need improved management if they are to be suitable as alternative feeding areas for brent geese.

The situation at Lindisfarne is more complicated. Lindisfarne acts as an important ice-winter 'refuge' for the majority of the population when the Danish waters freeze up in severe winters (Madsen 1984; Clausen et al. 1998). The present use of Lindisfarne during 'normal' winters, when half of the population use the site, leads to depletion of *Zostera* supplies to threshold levels in winter. This implies that if the whole population migrates to Lindisfarne in response to a severe Danish winter, they would encounter food limitation in the intertidal zone. Since there are few salt marshes found at Lindisfarne that could act as alternative feeding areas, nor are there alternative *Zostera* or salt-marsh areas near Lindisfarne which the geese could move on to (Perring & Walters 1977; Owen et al. 1986; own obs.), the geese would either have to switch to pastures on Holy Island or agricultural fields in Northumberland. This is not an unrealistic expectation—it actually happened both in 1995/96 and 1996/97 (Percival & Anderson 1998, this volume), causing conflicts with local farmers. Hence, the well-known damage-conservation conflict between farmers and grazing brent geese (eg. Madsen 1992) may also be relevant in future management decisions.

Given the shifts in distribution and habitat use witnessed in recent years, the population can only be safeguarded for the immediate future through integrated site management. With further increases in population size, the potential for conflict with agriculture may be expected to increase. Hence recommended guidelines for future management of the population should be compiled under an agreed international conservation plan.

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Choosing between feeding on *Zostera* and salt marsh: Factors affecting habitat use by brent geese in spring

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This study examines factors contributing to differences in habitat use by brent geese *Branta bernicla* in a spring staging area where they primarily feed on salt marshes and *Zostera marina* beds. Five years of study revealed significant year-to-year differences in the proportional use of the two main habitats, as well as three sub-habitats within the salt marshes. This study shows that the *Zostera* beds generally have a higher production than the *Puccinellia maritima* salt-marsh zone and that the brent geese react less to disturbance and fly less when feeding on *Zostera* beds compared to salt marshes. As the brent geese thereby expend less energy on an energetically costly activity, they favour the *Zostera* beds as feeding habitat. The salt marshes, on the other hand, act as important alternative feeding habitats for the brent geese, particularly in years with lower *Zostera* production (probably due to lower winter survival of *Zostera* shoots) or *Zostera* availability (due to high water levels). Large year-to-year variations in water level conditions have a major influence on brent goose habitat use. High water levels influence salt-marsh productivity negatively by flooding, limiting the number of days the brent geese can utilise *Zostera*. Under a future climate scenario, with increased water levels caused by global warming, it is likely that salt marshes will be lost. During periods with high water levels, the brent geese will then have to switch to feeding on agricultural areas.

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Introduction

Dark-bellied brent geese *Branta bernicla bernicla* wintering in Western Europe have traditionally used three coastal habitats: *Zostera* spp. beds, *Enteromorpha* beds and salt marshes (Mörzer Bruyns & Tanis 1955; Ranwell & Downing 1959). However, since the 1970s an increasing proportion of dark-bellied brent geese wintering in Britain and The Netherlands have used inland pastures and agricultural fields for feeding in mid-winter (especially winter wheat *Triticum aestivum* and in recent years oil-seed rape *Brassica napus*; Ebbsinge et al. 1981; Tubbs & Tubbs 1982; Round 1982; McKay et al. 1993). It is evident that the switch to salt marsh and inland feeding takes place when food resources in the intertidal *Zostera* and *Enteromorpha* beds become depleted (Charman 1979; Tubbs & Tubbs 1983; Madsen 1988; Summers 1990); and evidence has recently been compiled which shows that the dark-bellied brent geese leave the salt marshes in mid-winter to feed on inland habitats, when food resources on the salt

marshes have been depleted as well (Vickery et al. 1995).

In spring brent geese again switch to feeding in the coastal zone, particularly on salt marshes. This probably reflects reduced food availability in *Zostera* and *Enteromorpha* beds over winter (Tubbs & Tubbs 1983; Summers 1990). Historical evidence suggests that brent geese prefer *Zostera* spp. beds and other seagrass beds as feeding habitat in spring when available (Lind 1956; Salomonsen 1957; Madsen 1985). Although many brent geese in Britain and in the Dutch-German-Danish Wadden Sea primarily use salt marshes in spring (Charman & Macey 1978; Ebbsinge et al. 1981; Summers & Critchley 1990), some use pastures managed for brent geese and even more switch to pastures during cold spring periods in the Netherlands (Ebbsinge 1992). Brent geese have recently started to use pastures in the Danish Wadden Sea (Madsen et al. 1990) and in the German Wadden Sea (Prokosch 1991) too.

Within the salt marshes, the geese particularly use three different vegetation zones: areas dominated by *Puccinellia maritima*, areas dominated by

Festuca rubra, and mosaic areas with a mixture of *Puccinellia*, *Festuca*, and the halophytes *Plantago maritima*, *Triglochin maritima*, *Aster tripolium* and *Spergularia* spp. The timing of use of these three zones is primarily regulated by spring weather conditions (Madsen 1989; Prop & Deerenberg 1991).

This paper assesses factors influencing brent goose habitat choice in spring when, in addition to feeding on salt marshes, the geese also have access to submerged perennial *Zostera marina* beds.

Study area and methods

The study was conducted during the spring from 1989 to 1993. The brent geese studied come from the Svalbard breeding population of light-bellied brent geese *Branta bernicla hrota* of which 50–75% used the study area around Agerø, in the western Limfjord, Denmark (Fig. 1) throughout spring in recent years (Clausen et al. 1998). Staging geese in the area roosted communally northwest of the island of Agerø and dispersed to feed on submerged *Zostera* beds, salt marshes, and (rarely) spring barley fields during the day.

The geese used an area including a total of 12.0 km² of *Zostera* beds and 7.5 km² of salt marshes (Fig. 1; Drachmann et al. 1993, and P. Clausen unpubl. data). The most important *Zostera* feeding area for brent geese was situated southwest of Agerø, and the most important salt marsh feeding site was located on northwest Agerø (Jørgensen et al. 1994) (Fig. 1). These two sites were chosen for studying time budgets, vegetation sampling, and dropping counts (on salt marshes).

The vegetation of the salt marshes was dominated by *Puccinellia maritima* (lower marsh), and *Juncus gerardii* and *Festuca rubra* (higher marsh). Locally abundant supplies of halophytes such as *Plantago maritima*, *Aster tripolium*, *Spergularia media*, and *Triglochin maritima* were found in mosaic areas, with *Juncus* and the halophytes growing in tussocks and *Puccinellia* in between. Eighty-nine percent of the salt marsh area was grazed by cattle (Clausen & Percival 1998, this volume) and may be considered as high quality for feeding brent geese (cf. Ebbsing 1992).

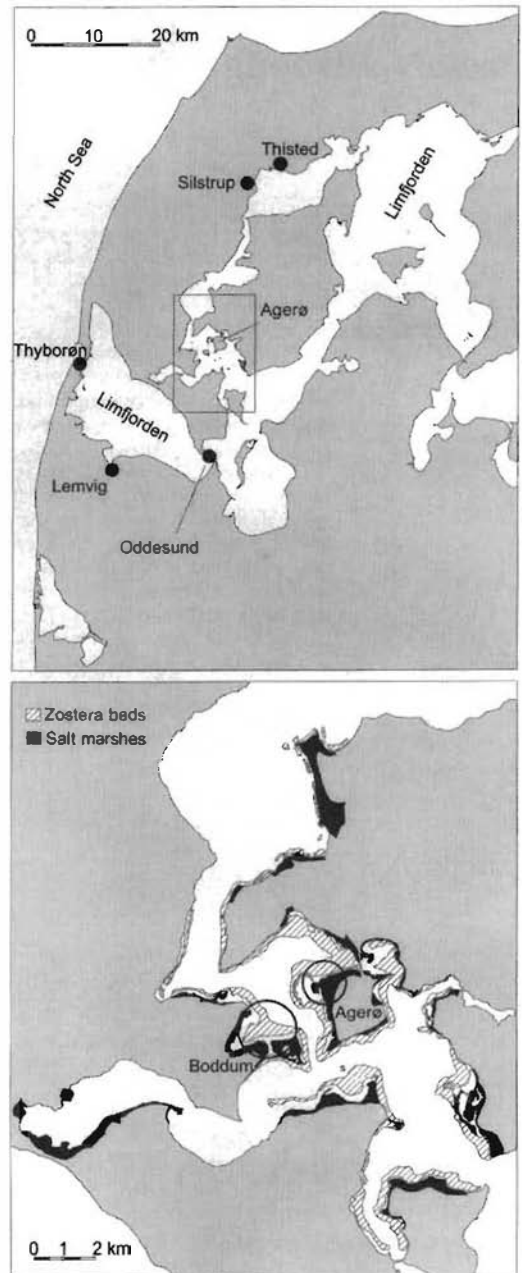


Fig. 1. The study area around Agerø in the western Limfjorden, northwest Denmark. The upper large scale map with dots indicating Thyborøn (the opening of Limfjorden to the North Sea), Lemvig and Thisted (from which water level measurements were obtained), and the meteorological station at Silstrup (from which measurements of temperature, radiation and precipitation were obtained). The lower detailed map shows the area used by brent geese roosting at Agerø, with salt marshes (black) and *Zostera* beds (hatched). Encircled are the most important *Zostera* bed near Boddum, southwest of Agerø, and the most important salt-marsh area on northwest Agerø.

Weather conditions

Daily observations of weather, mean temperature, global radiation (a measure of the solar radiation available for plant photosynthesis being calculated from hours of bright sunshine) and precipitation were obtained from a nearby meteorological station, Silstrup (Fig. 1) (Olesen 1990, 1991, 1992, 1993a; Plauborg & Sørensen 1994).

Based on mean temperatures, the T-200 date was used as an index of the relative start of growth on the salt marshes (Madsen 1989). T-200 is the date on which the sum of daily mean (positive) temperatures, summed from 1 January, exceeds 200°C.

Water levels, salt marsh floodings, and *Zostera* feeding

The tidal amplitude in western Limfjorden is on average 21 cm, but changes in wind direction, wind speed, and atmospheric pressure induce large changes in water level (Clausen 1994). Alternations in water level have two potential effects on habitat use by the brent geese: high water levels renders the *Zostera* beds inaccessible to feeding brent geese (Clausen 1994) and very high water levels flood the salt marshes.

Estimates of average daily water levels (ADWL; measured relative to DNN, 'Danish Ordnance Datum') were obtained from Lemvig Harbour (September 1988 to September 1992) and Thisted Harbour (September 1991 to May 1993). Water levels at Lemvig and Thisted are highly significantly correlated, and thus both reflect water levels found around Agerø (see Clausen 1994, where a full analysis of water level in relation to habitat use of the geese is given). An aerial photograph taken on 11 April 1982 showed that the lower *Puccinellia* zone of the northwest Agerø salt marshes was flooded on that date. The whole salt marsh was flooded on 25 March 1990 (personal observations). ADWL on these dates were 52.5 cm DNN and 85 cm DNN, respectively. The minimum number of flood days in all five seasons was thus estimated by the number of days with ADWLs between 52.5 cm and 85 cm DNN (lower salt marsh (only) flooded) and above 85 cm (whole salt marsh flooded), and the maximum

number of days without floodings as the number of days with ADWLs less than 52.5 cm.

Brent geese only fed on *Zostera* beds when water levels were sufficiently shallow; they switched to feeding on land at a certain water level, termed c_2 , which can be estimated by use of an approximate linear regression model (a full analysis is given by Clausen 1994, summary in the Appendix to this paper). Consequently the use of *Zostera* beds in spring could be influenced by differences in ADWL on count days. However, as the brent geese switched between feeding on the fjord and on land at significantly different water levels in the five springs (Clausen 1994, see Appendix), a correction was made for this by scoring the number of count days with ADWL below c_2 (from Clausen 1994, see Appendix) as 'fjord feeding days' and the number of count days with ADWL above c_2 as 'land feeding days' for each period (periods defined below).

Mappings of geese and vegetation

In 1989–1990 and 1992–1993 three to six counts were made each week of all brent geese in the study area from the last week of March until the end of May; in 1991 one to four counts were made per week. A full count of the area was usually made with telescope from eight observation posts in less than three hours. Positions of flocks and numbers of geese were drawn on field maps (scale 1:25,000).

To determine goose preferences of salt-marsh habitats, the salt marshes were mapped at the end of May 1990. Salt marshes were divided into three sub-habitats, *Puccinellia* dominated areas (more than 2/3 of *Puccinellia* zone), *Juncus/Festuca* dominated areas (more than 2/3 of *Juncus/Festuca* zone), and mosaic areas (intermediate). Mapping was achieved by walking through the whole area and drawing the information collected directly on field maps. The salt-marsh habitat use by the geese was then quantified by superimposing the goose count maps over the salt-marsh habitat map and assigning each observed goose flock to sub-habitat.

For all counts, the brent geese flocks feeding on *Zostera* were summed. Flocks of brent geese feeding on land were divided into those feeding in *Puccinellia*, mosaic, *Juncus/Festuca* salt-marsh areas, and spring barley fields (used only occa-

sionally by the geese). The differential use of the different habitats for each spring was then calculated as the sum of observed individuals in each habitat.

Throughout this paper, the spring staging period, subjectively taken as 21 March to 31 May, was divided into two periods of 5 weeks each, i.e. the early spring period (21 March–25 April) and the late spring period (26 April–31 May).

Time budgets

When feeding on the salt marshes around Agerø, brent geese were highly mobile and moved among different salt marshes throughout the day, with small or large flocks coming to and from any site under continuous observation. Hence compilation of a time budget based on a single 'flock' from dawn to dusk was impossible. Time budget bouts of one to eleven hours of continuous observation spread throughout the day were made on brent geese flocks feeding on *Zostera* as well as on the salt marsh from mid-April to mid-May 1990–1993. Time budgets were made by instant scans of the observed flock every 15 minutes (Altmann 1974), dividing the flock into individuals engaged in feeding, roosting, preening, walking, swimming, flying, drinking, alertness, and aggressive encounters. In addition, disturbances, the source of disturbance and the reaction of the geese (proportion of flock flying up) were recorded for each 15-minute period.

Goose use, standing crop and NAPP of salt marshes

The timing and intensity of goose use of north-western Agerø salt marshes was studied by counting goose droppings along a transect of permanent circular plots (2 m radius), which were centrally marked by small wooden pegs in 1989, 1990 and 1993. The plots were placed at 10-m intervals in a mosaic sward. The percentage coverage of *Puccinellia* zone and *Juncus/Festuca* zone, respectively, was estimated to the nearest 5% in each plot. In 1990 and 1993, droppings were counted and removed at every two weeks from the end of March to late May. As weekly counts were

made in 1989, counts from every other week that year were summed. This methodological change is considered of minor importance because individual faeces are recognisable for at least 3–4 weeks, even after heavy rainfall (J. Madsen unpubl. data) and salt marshes were not flooded during the sample period (results below).

Standing crop in the *Puccinellia* zone along the transect was measured on three occasions in 1989 and 1993, and twice in 1990. On each sampling occasion, grass turves were sampled randomly; in 1989 and 1990 three samples sized 0.07 m², and in 1993 six samples sized 0.02 m². In the laboratory, vegetation was clipped to the soil surface and washed, and living material was sorted into plant species. In 1993, dead above-ground plant material was also sorted and removed. Samples were dried at 80°C for 24 hours, cooled in an dessicator and weighed.

The net above-ground primary production (NAPP) along the grazed transect was estimated by the amount of vegetation sampled and the amount consumed by the geese,

$$\text{NAPP} = x_f - x_i + C$$

where x_i is the biomass (live + dead) present at the start of the season, x_f is the biomass (live + dead) remaining after the departure of the geese, and C is the forage consumed (Cargill & Jefferies 1984). Dead biomass in 1989 and 1990 was estimated on the assumption that the ratio of dead:live material was similar to that found in 1993. C was calculated from the cumulative number of droppings in sampled plots and the retention rates of the food plants after gut passage. Retention rates of *Puccinellia* was taken as 25% in April and 32% in May (after Madsen 1989). Calculations were based on dryweights of four samples of 30 fresh droppings collected along the transect, dried at 80°C for 24 hours, cooled in a dessicator and weighed.

Goose use, standing crop and NAPP of *Zostera* beds

Zostera was sampled in a grazed study area in the *Zostera* bed southwest of Agerø (Fig. 1) on two occasions in 1992 and three in 1993 during early April to late May. Samples were taken by placing a 0.1 m² square steel frame on the bottom; *Zostera* plants growing inside the frame but flattened when

the frame was placed were gently pulled inside, and plants growing outside were likewise pulled out. A square of *Zostera* turf was cut along the inside of the frame, and all the turf removed to the surface in a sieve (1 mm mesh). All samples were sieved in saltwater, and the resulting material collected in plastic bags. In the laboratory, samples were sorted into vegetative shoots, flowering shoots, rhizomes, and dead material. The number of live shoots was counted, and all fractions were dried to constant weight at 70°C in an oven and weighed.

Additional data on *Zostera* biomass was obtained from the same area, collected during a study of population dynamics of *Zostera marina* in spring 1990 (Olesen 1993b; Olesen & Sand-Jensen 1994a, 1994b).

For each count the number of brent geese feeding within the sampled *Zostera* bed were extracted, and the number of goose-days used there was calculated. The number of goose-days between two counts was calculated as the average number of geese observed at the two counts multiplied by the number of days between them; the calculated goose-days were then summed to give the total number of goose-days (G) used over the entire period.

The total area of the sampled *Zostera* bed is 845,800 m² (Drachmann et al. 1993). Only part of this is available to feeding brent geese, because brent geese only can reach 40 cm below surface when feeding (Clausen 1994). Since water level rarely falls below -30 cm DNN (Clausen 1994), only *Zostera* found at water depths of approximately 0–70 cm is usually available to feeding brent geese. Since 7 of 34 plots sampled plots in a 100 × 300 metre grid within the *Zostera* bed occurred in this water depth range (0–70 cm, corrected for deviations from 'normal' i.e. 0 cm DNN; J. Drachmann, S. Mark & P. Clausen, unpubl. data), the *Zostera* area available to feeding brent geese, Z_a , was estimated as:

$$Z_a = 7/34 \times 845,000 \text{ m}^2 = 174,100 \text{ m}^2$$

The consumption of *Zostera* m⁻², C, was calculated as

$$C = (G/Z_a) \times \text{GIR}_d \times D \times P_f$$

where G and Z_a are as defined above, GIR_d is the intake rate for brent geese feeding on *Zostera* (0.22 g dryweight min⁻¹; from Clausen 1994), D is the average day length (min day⁻¹), and P_f is the

proportion of the day length used for feeding by brent geese (0.784, from time budgets; see below).

Estimates of NAPP in the grazed *Zostera* bed were again calculated by use of Cargill & Jefferies (1984) formula,

$$\text{NAPP} = x_f - x_i + C$$

where x_i is the vegetative and flowering shoot biomass present in early spring, x_f is that present in late spring (after departure of the geese), and C is the amount consumed by the geese as defined above.

This approximation of NAPP does not include changes in dead above-ground biomass and will probably give an underestimate. Dead biomass was excluded because a great number of leaves are lost by wave action or shedding (a natural habit of *Zostera* by which loading of epiphytes are reduced; Sand-Jensen 1977). These may float around and decompose elsewhere in the *Zostera* bed, accumulate and decompose in deeper parts of Limfjorden, or wash onto surrounding beaches to decompose there. Consequently, changes in dead biomass within the sample area might represent *Zostera* produced elsewhere and introduce an inexpedient error in the NAPP estimate. Acknowledging this limitation of the calculations, the resulting NAPP estimates will be termed residual net above-ground primary production rNAPP.

Results

Weather conditions

All five springs followed very mild winters, with monthly average temperatures more than 2°C above normal in January–March of all years (except February 1991). Monthly average temperatures in April 1990, May 1992 and May 1993 were more than 1°C above normal, and May 1991 less than 1°C below normal (Table 1). These differences in temperatures resulted in highly different cumulative temperatures, with T-200 ranging from 6 February (1989) to 25 March (1991) (Fig. 2), equivalent to a 47-day difference in onset of growth on the salt marshes between the warmest and coldest study years.

Solar radiation was similar in all years, deviating less than 25% from normal in most months

Table 1. Summary of weather conditions around Agerø January–May, 1989–1993, based on measurements from a nearby meteorological station, Silstrup (Fig. 1). Normal values are average values of data for 1961–1990. Data from Olesen (1990, 1991, 1992, 1993a) and Plauborg & Sørensen (1994).

	Month	Year					Normal 1961–1990
		1989	1990	1991	1992	1993	
Temperature (°C)	January	5.5	4.3	2.3	3.5	2.3	0.2
	February	4.6	5.4	−1.0	3.9	1.9	−0.1
	March	5.2	5.9	3.7	3.9	2.9	1.8
	April	5.4	7.0	6.1	5.2	6.9	5.3
	May	10.2	11.2	8.5	12.6	11.8	10.3
Global radiation (MJ/m ² /month)	January	42	38	57	55	54	47
	February	90	96	110	100	113	105
	March	208	270	200	200	267	229
	April	413	455	400	356	427	396
	May	655	626	662	659	653	551
Precipitation (mm/month)	January	39	142	85	56	104	70
	February	108	150	36	39	28	49
	March	130	52	55	89	27	58
	April	43	38	54	55	22	45
	May	50	15	13	40	13	55

(Table 1). The cumulative solar radiation curves were consequently quite similar, adding up to between 1370 and 1511 MJ/m² by the end of May (Fig. 2).

Precipitation was highly variable in the five years, both in timing and amount. All years experienced cumulative rainfall at or above normal; 1990 had extremely heavy rainfalls in February, and 1992 through March–April, whereas 1989, 1991 and 1993 were drier years compared to 1990 and 1992 (Table 1, Fig. 2).

df = 8, $P > 0.10$), whereas a significant difference was found for the late winter and spring period (1 January–31 May) ($\chi^2 = 47.47$, df = 8, $P < 0.001$) (Table 2). Year-to-year comparisons found a higher number of days with flooding of the higher salt marsh in 1990 and 1993, compared to 1989, 1991 and 1992; and flooding of the lower salt marsh can be ranked with 1990 highest, followed by 1993, 1989 and 1991, and 1992 lowest (Table 2).

Water levels and salt-marsh floodings

Water levels fluctuated greatly in all five winters and springs with ADWL ranging from −76 cm to 167 cm during 1 September–31 May, 1988–1993 (Fig. 3).

Salt marshes flooded regularly during westerly storms from September until March, whereas no floodings occurred during April and May. In autumn and early winter (1 September–31 December), there were no significant differences between the number of days with unflooded salt marsh, lower salt marsh (only) flooded, and whole salt marsh flooded, in the five years ($\chi^2 = 13.24$,

Goose numbers and differential habitat use

The Agerø area was used by 2200 to 3100 brent geese throughout the spring staging period, 1989–1993 (Table 3). The number of geese found in the area within a single spring was fairly constant. All counts covering the whole study area deviated less than 5% from the maximum number recorded that spring (Clausen 1991 and unpubl.).

The brent geese showed highly significant differences in their use of the three habitats, (*Zostera* beds, salt marshes and spring barley fields) in early and late spring periods in all years (pairwise comparisons between all years/periods by χ^2 tests, all $\chi^2 > 214.14$, $P < 0.001$) (Table 3).

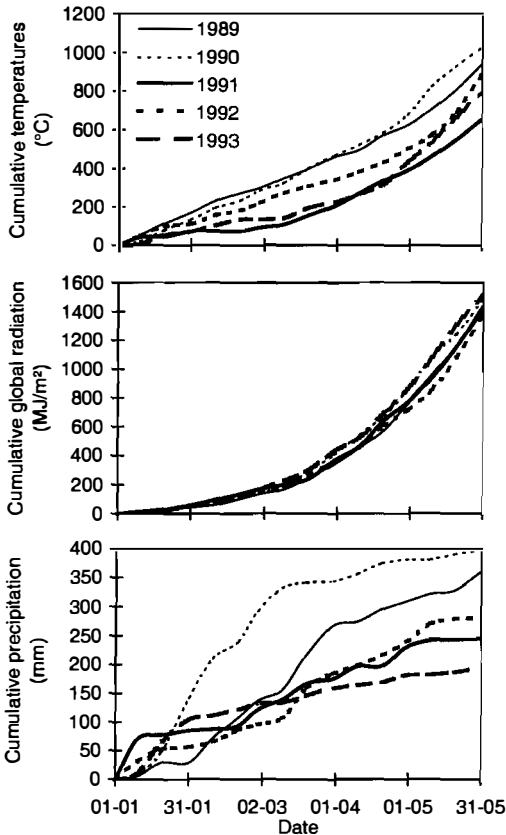


Fig. 2. Cumulative curves of average temperatures, global radiation and precipitation, springs 1989–1993 at Silstrup meteorological station, near Agerø.

The predominant use of salt marshes in the early spring periods of 1989 and 1993 is a contrast to an almost even use of *Zostera* beds and salt marshes in the other years. In the late spring periods, the predominant use of salt marshes in 1989 and 1990, and to some extent 1993, contrast the more even use of *Zostera* beds and salt marshes in 1991 and 1992. The relatively high use of barley fields in spring 1991 was unusual (the first year recorded to this extent, according to the local farmers).

The proportional use by brent geese of the three habitats within the salt marshes was highly significantly different in the early and late spring periods in all years (All $\chi^2 > 173.10$, $P < 0.001$), with a proportionally low use of *Puccinellia* zone salt marsh in early spring 1990, high use of *Juncus/Festuca* zone in early and late spring 1991, and

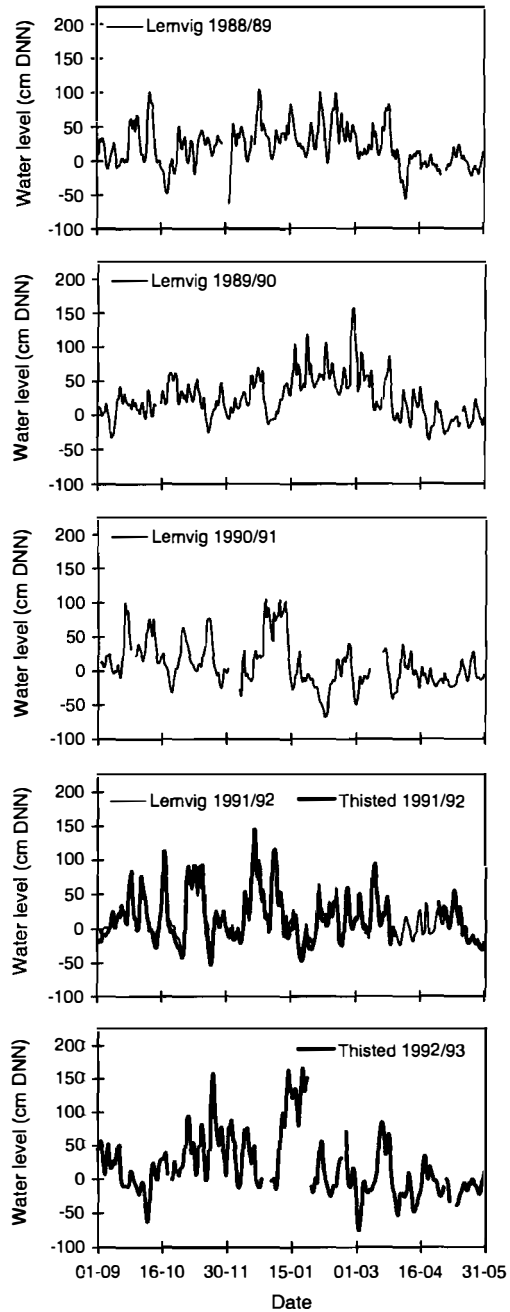


Fig. 3. Water level fluctuations in the western Limfjorden, September through May, 1988/89–1992/93.

high use of mosaic areas in early spring 1990, and late spring 1989 and 1990 (Table 3).

Table 2. Estimates of the maximum number of days without floodings and minimum number of days with floodings of the Agerø salt marshes 1 September–31 May, 1988/89–1992/93. For each season flooding was separated into the periods prior to and after 1 January. These were further divided into days with floodings of the whole salt marsh and those with floodings of the lower salt marsh (only).

		1 September–31 December			1 January–31 May		
Season		Unflooded	Whole salt marsh flooded	Lower salt marsh flooded (only)	Unflooded	Whole salt marsh flooded	Lower salt marsh flooded (only)
1988/90	Lemvig	103	3	11	129	2	17
1989/90	Lemvig	108	0	11	112	12	26
1990/91	Lemvig	92	4	16	132	3	8
1991/92	Lemvig	91	4	19	143	3	5
1992/93	Thisted	87	6	20	114	16	12

Water levels and *Zostera* feeding

‘switch’ water levels (c_2) estimated (Clausen 1994, see Appendix to this paper).

A significant correlation between habitat use and water level was found in eight spring periods, and

The proportional brent goose use of *Zostera* beds was significantly correlated with the proportions of count days with water levels below c_2 (on

Table 3. Habitat use by brent geese within the Agerø area in early and late springs, 1989–1993. ‘Geese staging’ gives an approximate number of geese which stayed in the area throughout each spring. ‘Geese counted’ represents the sum of individuals with known habitat use for each period. Their proportional habitat use, as well as the proportional sub-habitat use of those using salt marshes are tabulated for each period.

		Year				
		1989 2200	1990 2200	1991 2600	1992 3100	1993 2600
Geese staging in spring						
Early spring	(21 March–25 April)					
Switch water level (c_2) (cm) ¹		–10.65	7.92	–15.80	3.89	–9.62
Geese counted		25,289	24,722	12,259	45,944	43,973
Proportional habitat use	<i>Zostera</i> beds	27.1	58.3	46.6	51.1	29.4
	Salt marshes	72.5	41.7	47.7	48.9	70.6
	Spring barley fields	0.4	0	5.7	0	0
Proportional salt marsh	sub-habitat use					
	<i>Puccinellia</i>	53.0	20.4	34.1	50.2	45.1
	Mosaic	16.3	46.9	19.7	15.8	21.5
	<i>Juncus/Festuca</i>	30.6	32.7	46.2	34.0	33.4
Late spring	(26 April–31 May)					
Switch water level (c_2) (cm)		–	–	0.82	–11.34	–28.15
Geese counted		22,218	16,765	15,823	75,186	105,980
Proportional habitat use	<i>Zostera</i> beds	16.0*	14.8	56.7	43.3	38.3
	Salt marshes	84.0	85.2	36.6	55.5	61.7
	Spring barley fields	0	0	6.7	1.2	0
Proportional salt marsh	sub-habitat use					
	<i>Puccinellia</i>	44.7	46.7	51.8	63.8	53.6
	Mosaic	44.6	34.9	10.9	11.8	18.5
	<i>Juncus/Festuca</i>	10.7	18.3	37.3	24.4	27.9

¹ c_2 values were taken from Clausen (1994: see also Appendix to this paper). There was no relationship between water level and habitat use in late spring 1989 and 1990.

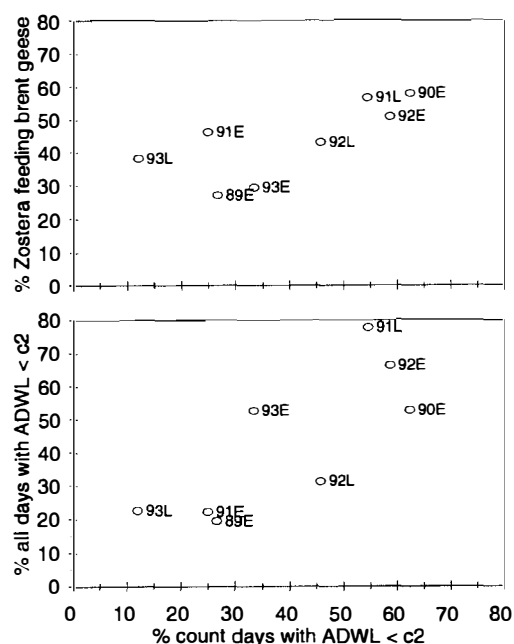


Fig. 4. The upper graph gives the relationship between the proportion of count days with average daily water levels below the 'switch' water level c_2 (i.e. predicting that the brent geese should feed on *Zostera*) and the proportion of brent geese actually observed feeding on *Zostera*. The lower graph gives the relationship between the proportion of count days with average daily water levels below the 'switch' water level c_2 and the proportion of all days with average daily water levels below c_2 . Numerals and letters gives the year and period (E = early, L = late) respectively.

which the brent geese could be expected to feed on the fjord, as predicted from the water level in Limfjorden) (Spearman rank correlation, $r_s = 0.81$, $n = 8$, $P < 0.05$) (Fig. 4). The proportions of count days with water levels below c_2 were highly significantly different in the eight spring periods ($\chi^2 = 17.60$, $df = 7$, $P < 0.025$), i.e. the observed significant within-year and year-to-year differences in *Zostera* use may reflect the differences in water levels in the different study periods.

To test whether water levels on count days were representative of water levels over the whole period, the proportion of days with ADWL below c_2 (on count days) were compared with the proportion of days with ADWL below c_2 (all days). The test revealed that the proportion of count days within each period with water levels

below c_2 was significantly correlated with the proportion of all days with water levels below c_2 (Spearman rank correlation, $r_s = 0.74$, $n = 8$, $P < 0.05$) (Fig. 4). Hence, water levels recorded on count days may be considered as representative for water levels in the whole period.

Time budgets

A total of 216 scans were made on flocks feeding on salt marshes and 105 scans on *Zostera* beds. Flocks under observation on salt marshes were significantly more variable in size and smaller than those observed on *Zostera* beds, with mean flock sizes of $694 (\pm \text{S.D. } 503)$ on salt marshes and $811 (\pm \text{S.D. } 327)$ on *Zostera* beds ($F_{215,104} = 2.36$, $P < 0.001$; Welch's approximate t-test, $t = -2.49$, $df = 293.1$, $P = 0.0132$).

Comparison of time budgets of salt-marsh and *Zostera*-feeding brent geese revealed no significant difference between the two habitats in the proportion of time spent in the two main activities, feeding and roosting, which together represented 93.2% and 97.2% of the time used in salt marshes and *Zostera* beds respectively (Table 4). However, brent geese feeding on salt marshes spent significantly more time flying, walking, being alert, and drinking, whereas there were no significant

Table 4. Proportion of time spent in different activities by brent geese feeding on *Zostera* beds and salt marshes, respectively (from time budgets).

Activity	Salt marsh feeding	<i>Zostera</i> feeding	t^1	Probability ¹
Feeding	76.5	78.4	-1.38	$P = 0.17$
Roosting	16.7	18.8	-0.71	$P = 0.48$
Flying	3.2	0.4	2.76	$P = 0.0062$
Walking ²	0.5	0		
Alert	1.8	0.05	13.75	$P < 0.0001$
Drinking ²	0.3	0		
Swimming	0.3	1.7	-0.69	$P = 0.49$
Preening	0.5	0.1	1.71	$P = 0.09$
Aggression	0.1	0.02	1.87	$P = 0.06$

¹ Tests and probabilities are t-tests based on arcsin transformed proportions (Student's t for equal variances, Welch's approximate t for unequal variances).

² Non-testable due to the fact that all observations in *Zostera* beds had 0 geese walking and drinking respectively.

differences in time spent on swimming, preening, and aggressive actions in the two habitats (Table 4).

There was no significant difference between the disturbance rate in the two habitats, i.e. 0.56 disturbances per hour in both. However, brent geese feeding on the salt marshes reacted more strongly when disturbed, with 84.5% of the flock flying up on salt marshes compared to 60.4% on *Zostera* beds (Student's *t*-test of arcsin transformed proportions, $t = 2.58$, $df = 43$, $P = 0.0132$). The most important disturbance source in both habitats were grey herons *Ardea cinerea* that flew to and from their feeding areas from a nearby heronry, with 63.3% of the disturbances caused by grey herons in salt marshes and 40.0% in *Zostera* beds (no significant difference between the proportions of grey heron disturbances and other disturbances in the two habitats, $\chi^2 = 1.36$, $df = 1$, $P > 0.1$, χ^2 test with Yates correction for continuity). Other sources of disturbance were goshawks *Accipiter gentilis*, farmers, and foxes *Vulpes vulpes* (on salt marshes), fishermen (on *Zostera* beds), and aircraft (both habitats). When disturbed by grey herons, 82.7% of brent geese feeding on salt marshes flew up in contrast to 46.2% of *Zostera* feeding geese ($t = 2.70$, $P = 0.0126$).

Goose use, standing crop and NAPP of *Puccinellia*

Brent goose use assessed by cumulative goose dropping densities on the salt marsh along the transect on northwest Agerø was significantly different between 1989, 1990 and 1993, with highest utilisation in 1989 and lowest in 1990 (Fig. 5).

The transect was dominated by *Puccinellia* in all years, but also comprised considerable amounts of *Juncus/Festuca* (i.e. on average 62.9% *Puccinellia* in 1989, 53.2% in 1990, and 62.2% in 1993). As some pegs disappeared between seasons, some circles were not exactly identical along the transect from year-to-year. However, the observed difference in goose utilisation could not be explained by a difference in *Puccinellia*:*Juncus/Festuca* ratio (no significant year-to-year differences; one-way ANOVA on arcsin transformed proportions, $F_{2,47} = 0.74$, $P = 0.4813$).

Live above-ground *Puccinellia* biomass on

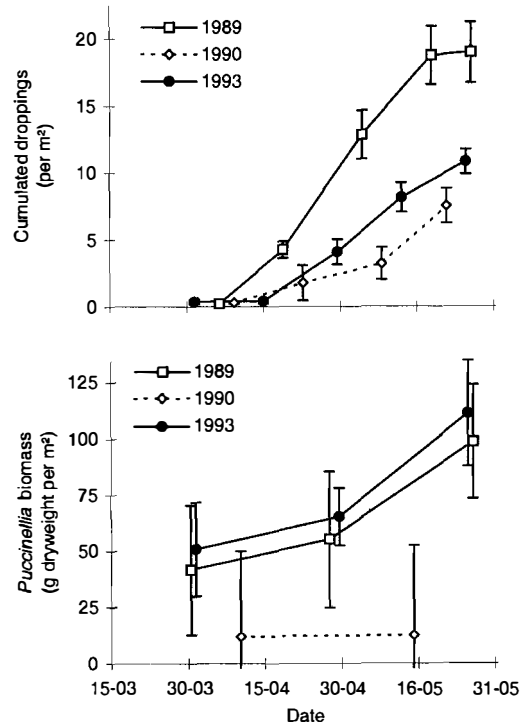


Fig. 5. Cumulative goose droppings (upper) and *Puccinellia* biomass (lower) on the northwest Agerø salt marsh, spring 1989, 1990 and 1993. The curves give average values \pm 95% confidence intervals.

sample dates was highly significantly different (two-way ANOVA, model year and date, $F_{7,25} = 17.65$, $P < 0.0001$) (Fig. 5). This was due to significant year-to-year differences in biomass in the three study years (one-way ANOVA, model year, $F_{2,25} = 12.02$, $P < 0.0001$), with a lower biomass in 1990 compared to 1989 and 1993 (Tukey *q*-test's, $P < 0.05$), whereas no significant difference was found between 1989 and 1993 (Tukey *q*-test; $P > 0.05$). Further to this, within-year increases in *Puccinellia* biomass occurred during spring 1989 (one-way ANOVA, model date, $F_{2,6} = 8.50$, $P = 0.0178$) and spring 1993 ($F_{2,15} = 17.22$, $P < 0.0001$), whereas no increase was detected in spring 1990 ($F_{1,4} = 0.02$, $P = 0.8893$) (Fig. 5).

The higher brent goose use of the *Puccinellia* marsh in 1989, combined with the similarity of above-ground biomass in 1989 and 1993, suggest that NAPP in the *Puccinellia* zone was slightly

Table 5. Estimates of net above-ground primary production (NAPP) in the northwest Agerø *Puccinellia* salt marsh zone springs 1989, 1990, 1993, based on estimates of goose consumption and biomasses early and late in spring. Values of live and dead biomasses and consumption are means (\pm S.E. in brackets).

Year	Period	Live biomass		Dead biomass		Increment in biomass		Consumption by		NAPP g m ⁻²
		(start)	(end)	(start)	(end)	(live + dead)		brent geese		
		g m ⁻²	g m ⁻²	g m ⁻²	g m ⁻²	g m ⁻²		g m ⁻²		
		\bar{x}_i	\bar{x}_f	\bar{x}_i	\bar{x}_f	$\bar{x}_f - \bar{x}_i$		C		$\bar{x}_f - \bar{x}_i + C$
1989	31 March–27 May	41.4 (32.4–50.5)	98.6 (90.6–106.6)	6.1 ²	8.2 ²	59.3		26.7 (25.1–28.2)		85.9
1990	10 April–15 May ¹	11.9 (10.8–13.0)	12.5 (9.6–15.5)	1.6 ²	1.2 ²	0.3		10.8 (9.5–12.0)		11.1
1993	1 April–26 May	50.7 (42.6–58.8)	111.2 (102.1–120.3)	7.4 (6.3–8.5)	9.2 (8.7–9.7)	62.3		15.3 (14.4–16.2)		77.7

¹ Consumption based on the period 10 April–22 May 1990.

² Dead biomass in 1989–1990 was estimated on the assumption that the live:dead ratio in these years were similar to that found in 1993.

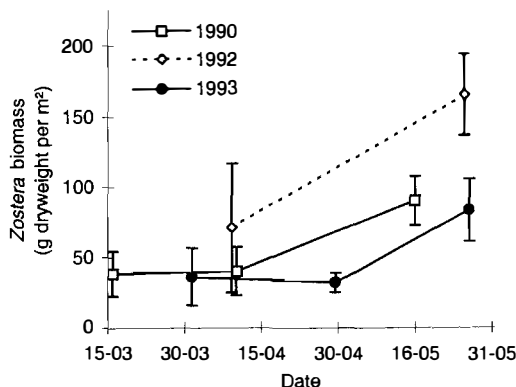


Fig. 6. The development in *Zostera* above-ground vegetative shoot biomass in the *Zostera* bed southwest of Agerø, spring 1990, 1992 and 1993. The curves give average values \pm 95% confidence intervals.

higher in 1989 than in 1993 (Table 5). The NAPP in 1990 may have been less than 25% of that found in 1989 and 1993 (Table 5).

Goose use, standing crop, and rNAPP of *Zostera* beds

Vegetative *Zostera* shoot biomass on sample dates was highly significantly different (two-way ANOVA, model year and date, $F_{7,63} = 23.34$, $P < 0.001$) (Fig. 6). This was due to significant year-to-year differences in biomass in the three study years (one-way ANOVA, model year, $F_{2,63} = 28.06$, $P < 0.0001$), with 1993 lowest in biomass, 1990 intermediate, and 1992 highest in biomass (all year-to-year comparisons significantly different, Tukey q-test's, $P < 0.05$). In addition to this there was a significant increase in vegetative *Zostera* biomass during all three springs (1990 one-way ANOVA, model date, $F_{2,48} = 26.34$, $P < 0.001$; 1992 $F_{1,6} = 30.66$, $P = 0.0015$; 1993 $F_{2,9} = 25.65$, $P = 0.002$).

The general increase in the number of brent geese that use the *Zostera* beds around Agerø has resulted in increasing *Zostera* biomass being grazed by brent geese in spring. Although there was less biomass in 1993 than 1990, some of the difference is caused by the grazing brent geese. Nevertheless, rNAPP in 1993 was apparently only

Table 6. Estimates of residual net above-ground primary production (rNAPP) in the *Zostera marina* bed southwest of Agerø springs 1990, 1992, 1993, based on estimates of goose consumption and live biomasses (vegetative and flowering shoots) early and late in spring. Live biomass values are means (\pm S.E. in brackets).

Year	Period	Bird-days used in the <i>Zostera</i> bed	Vegetative biomass (start) g m^{-2} x_i	Vegetative biomass (end) g m^{-2} x_f	Flowering biomass (start) g m^{-2} x_i	Flowering biomass (end) g m^{-2} x_f	Increment in biomass (vegetative + flowering) g m^{-2} $x_f - x_i$	Consumption by brent geese g m^{-2} C	rNAPP g m^{-2} $x_f - x_i + C$
1990	1 April–27 May ¹	16,356	39.5 (31.7–47.3)	118.5 (109.7–127.3)	0	15.0 (6.2–23.8)	94.0	14.3	108.3
1992	9 April–26 May	23,123	34.5 (20.1–48.9)	165.0 (156.0–174.1)	0	9.9 (7.2–12.6)	140.4	21.0	161.4
1993	1 April–27 May	26,892	36.3 (29.9–42.6)	82.8 (75.8–89.8)	0	5.1 (2.8–7.3)	51.0	23.8	74.8

¹ Biomass on 1 April was estimated by interpolation between samples from 15 march and 10 April, and on 27 May between samples from 16 May and 29 June, 1990.

about 50% of that in 1992, with 1990 intermediate (Table 6).

Discussion

Annual variations in habitat use of the brent geese

This study found large within-year and year-to-year variations in brent goose habitat use around Agerø.

Use of *Zostera* beds as feeding habitat was significantly correlated with the proportion of count days on which the brent geese could be expected to feed on *Zostera*, as predicted from the water level. This suggests that the brent geese will feed on the fjord as soon as water levels permit them to do so. Hence, *Zostera* should be considered the preferred habitat in spring, because if the brent geese preferred the salt marshes, there would be no reason to switch to the *Zostera* beds when the water level fell. This conclusion holds for the early spring period of all years and the late spring period 1991, with very strong correlations found between water level in Limfjorden and habitat use of the brent geese (Clausen 1994, see Appendix to this paper). The situation in late spring is more complicated, with no correlation between water level and habitat use in the late spring periods of 1989–1990, and with less clear correlations in the late spring periods of 1992–1993 (Clausen 1994). This difference between the early and late spring periods may be caused by a combination of falling nutritional value of *Zostera*, combined with increasing availability of high quality food plants such as *Triglochin*, *Plantago*, *Aster* and *Spergularia* on the salt marshes (Clausen 1994).

Water levels on count days were representative of water levels for the whole period, so observed differences in the proportional use of *Zostera* beds (ranging from 27% to 58% in early spring periods) may be considered as genuine year-to-year variations, i.e. water level fluctuations relative to 'switch' water levels in some years give the brent geese high access to feeding on *Zostera*, in other years low access.

Annual variations in goose use of salt marsh zones and salt marsh production

The lower salt-marsh zone and *Puccinellia maritima* have often been reported as the prime feeding habitat and food item, respectively, for salt-marsh feeding brent geese (e.g. Madsen 1989; Prop & Deerenberg 1991; Olff et al. 1992). Therefore the relatively low use of the *Puccinellia* zone by brent geese in early springs 1990 and 1991 may be considered as unusual. Madsen (1989) and Prop & Deerenberg (1991) likewise found considerable seasonal variations in *Puccinellia* production and brent goose use. The variations were induced by differences in spring weather conditions: reduced use of the *Puccinellia* zone and higher use of the *Festuca* zone occurred in cold springs with low standing biomass and low NAPP of the *Puccinellia*. This would explain the low use of the *Puccinellia* zone and high use of the *Juncus/Festuca* zone in the early spring period 1991, as well as the high use of the *Juncus/Festuca* zone in the late spring period 1991, the coldest spring studied. But the spring weather conditions fail to explain the low use of the *Puccinellia* zone in the early spring period 1990 which contrasts with the high use in 1989, as both these years had the warmest springs. Two lines of evidence may explain this inconsistency. Salt marshes were flooded much more in late winter 1990 than in 1989, and precipitation was much higher in late winter of 1990 than in any other of the years studied. Armstrong et al. (1985) showed that summer floodings and heavy rainfall caused depression of 'redox' potentials of *Puccinellia* salt-marsh soils, and they suggested that autumn and winter flooding and rainfall might induce more permanent low redox potentials (i.e. reducing, anoxic soils). Howes et al. (1981) found that water-logging and reduced soils inhibited *Spartina alterniflora* growth, and Armstrong et al. (1985) proposed this would be even more pronounced in *Puccinellia*, with its lower capacity to aerate soil around the roots with oxygen taken from the atmosphere, thus compensating for the anoxia of the soils, as compared to *Spartina*. Hence it is suggested that increased flooding and rain on Agerø salt marshes in late winter 1990 prolonged the period of water-logging on the lower salt marsh and depressed production. Later in spring, growth may have been hampered by the very high temperatures and insolation in April 1990, de-

hydrating lower salt marshes and consequently increasing soil salinity. Increasing salinities reduce the growth rates of many halophytic monocots, such as *Puccinellia* (Rozema 1991).

Compared to other years, the greater use of mosaic areas in the early spring period 1990 and in the late spring periods of 1989 and 1990 may result from the earlier and warmer springs of 1989 and 1990, because the halophytes *Triglochin*, *Plantago*, *Aster* and *Spergularia* start growing slightly later than the graminoids *Puccinellia*, *Juncus* and *Festuca*. No field data were collected on densities of *Triglochin*, *Aster*, *Spergularia* and *Plantago*, but it was my impression from field work on the salt marshes that 1990 was especially characterised by an early growth of the four halophytes in the mosaic areas, in contrast to the cold spring 1991 when only very few plants of these species could be found in the same areas even in mid-May.

Annual variations in *Zostera* production

It appears that 1993 had a lower *Zostera* production than 1992, with 1990 intermediate. This may result from differences in winter survival of *Zostera* shoots, as shoot densities in the three years can be ranked likewise, i.e. 748 ± 123 shoots m^2 (Mean \pm S.E., $n = 4$) in late March 1993, 1125 ± 123 ($n = 4$) in early April 1992, and ca. 825 ± 85 shoots m^2 ($n = 15$) in mid-March 1990 (P. Clausen, unpubl. data; Olesen & Sand-Jensen 1994a). Nevertheless, year-to-year variations in *Zostera* rNAPP were smaller than those of NAPP in the *Puccinellia* zone. This may be explained by a difference in the most important growth regulating factor in the two habitats. Variation in radiation explained 75% of the variation in growth rates of *Zostera marina* (Sand-Jensen & Borum 1983), whereas temperature is the most important growth regulator in terrestrial plants (Larcher 1980), and year-to-year variation in radiation was much less than variation in temperature in the study area.

Time budgets in salt marshes and on *Zostera* beds

Brent geese feeding in salt marshes used significantly more time flying, walking, being alert

and drinking than they did when feeding in *Zostera* beds. Predation risks are less in *Zostera* beds because predators (foxes and goshawks) found around Agerø could not successfully attack feeding brent geese on water. Hence, brent geese spend less time being alert in the *Zostera* beds, probably also because flocks feeding on *Zostera* are larger (cf. Inglis & Lazarus 1981). When disturbed, fewer birds react on *Zostera* beds, probably due to the greater safety provided by feeding on water. However, salt-marsh feeding brent geese spent eight times longer flying than those feeding on *Zostera*, and differences in reactions to disturbance can only account for less than a twofold increase. Brent geese feeding on salt marshes throughout the day make many small flights between different salt-marsh vegetation zones, between salt-marsh sites, over fences, and to and from drinking sites in small ponds on the salt marshes. *Zostera* feeding brent geese usually makes two daily flights, from the roost to the *Zostera* bed in the morning and back in the evening, and occasionally a single flight between two *Zostera* beds during the day. Apart from these movements, the *Zostera* feeding brent geese tend to gradually graze over the whole *Zostera* bed from one end to the other, without flying. They do not spend time drinking, probably because the *Zostera* ingested provides them with enough water, as *Zostera* contains on average 84% water ($n = 10$) (Clausen 1994), whereas *Puccinellia* only contains 69% (Prop & Deerenberg 1991).

Choosing between *Zostera* beds and salt marshes

There are three good reasons for the brent geese to feed on *Zostera* as soon as it becomes available. Firstly, intake rates and the metabolisable energy contents of *Zostera* are usually similar or higher than when the geese feed on salt marsh halophytes (Clausen 1994). Secondly, the geese fly less because the greater safety of feeding on water and the different exploitation patterns of the two habitats. The geese thereby save energy as flight is by far the most costly activity (i.e. $12.5 \times \text{BMR}$ in contrast to the other time budgeted activities ranging from 1.4 to $2.3 \times \text{BMR}$; Wooley & Owen 1978; Clausen 1994). In favour of this interpretation is the work by Riddington et al. (1996), who compared salt-marsh and pasture-feeding brent

geese. They demonstrate how brent geese must spend a considerable amount of additional time compensating for the lost food intake and increased energy expenditure when they use more time on flying (in their case due to disturbance). Thirdly, *Zostera* productivity is higher than in salt marshes. rNAPP estimates for the spring period for the *Zostera* bed southwest of Agerø were on average twice those found in the *Puccinellia* zone on northwestern Agerø. This is in agreement with annual production estimates of above-ground biomass in Danish *Zostera* beds ranging from 654 g m^{-2} to 1670 g m^{-2} ($n = 9$; Sand-Jensen 1975; Wium-Andersen & Borum 1984; Pedersen & Borum 1993; Olesen & Sand-Jensen 1994a) compared to annual above-ground production of *Festuca rubra*, *Puccinellia maritima*, *Juncus gerardi*, *Triglochin maritima* and *Plantago maritima* in Dutch salt marshes ranging from 70 g m^{-2} to 992 g m^{-2} ($n = 9$; Bakker et al. 1993).

Intake rates of brent geese in the different habitats are dependent on growth form, size, production, and available biomass of their food plants, and in the case of *Zostera* feeding, water level. Throughout their staging period, brent geese face daily changes in water level and weather conditions, factors which may favor feeding in either the *Zostera* beds or on the salt marshes and in different habitats within the salt marshes. On a given day, the available biomass on the salt marshes may be considered as constant, whereas that available in the *Zostera* bed fluctuates with the water level. An illustration of this situation is provided from the two years when biomass development and NAPP were monitored in both the *Zostera* bed and in the *Puccinellia* zone. In 1990 growth in the *Puccinellia* zone was very poor, and the brent geese grazed 97% of NAPP. In 1993, growth was higher, with NAPP being seven times that found in 1990, and the geese only grazed 20% of NAPP. In the *Zostera* bed the opposite situation occurred, with better growth in 1990 NAPP being 1.4 times that found in 1993. The response from the geese to this difference was that in early spring 1990 they switched to feeding on *Zostera* at a significantly higher water level (7.9 cm DNN) than in early spring 1993 (−9.6 cm DNN) (Clausen 1994, see Appendix to this paper).

The annual variations in productivity in the two habitats, as well as the fluctuations in water level, are highly dependent on weather conditions and thereby affect habitat use of the brent geese. In

some years, salt marshes may be a very important alternative to the *Zostera* beds for the feeding brent geese; in other years the marshes are less important. Nevertheless, when these two alternative feeding habitats are available, the brent geese in most years will most likely have a much better chance of achieving good condition in late spring. This may in fact be one very good reason behind the general belief that brent goose populations were much higher in the last century and at the start of this century (e.g. Salomonsen 1958). This was before the eelgrass 'wasting disease' almost wiped out *Zostera marina* in Western Europe (e.g. Rasmussen 1977). Having the salt marshes as the only feeding habitat in spring will lead to poor spring fattening conditions in some years (Prop & Deerenberg 1991) and thereby failed breedings (Ebbinge 1989).

A future perspective—brent goose habitat use under a global warming scenario

The findings of this study are particularly important in a future perspective, namely that of addressing the potential implications of global warming (due to increased emissions of carbon dioxide and so-called greenhouse gases) on habitat use of the brent geese.

Several scenarios of the expected influence of global warming on climate patterns exist, the more widely accepted of which are presented by IPCC (1990). All the IPCC scenarios predict that a series of climate changes will take place; in a Danish context these have been further developed by Laursen (1992). Firstly, temperatures are expected to increase during the whole annual cycle, particularly during winter. Secondly, precipitation will most likely increase, again particularly during winter. Thirdly, there may be an increased frequency of storms, again mostly during winter. In addition to these climate changes, mean sea water level is expected to rise, with an expected increase of more than 50 cm in Danish waters by year 2075 under the best assessment of IPCC (IPCC 1990; Jørgensen 1992).

An increase in water levels by 50 cm in the surroundings of Agerø would most likely permanently flood most of the present salt marshes, causing them to disappear. The *Zostera* beds could be expected to move closer to the present shore line, so the influence on these is perhaps less

important in a future management perspective, unless warmer summers have a negative influence on the *Zostera* distribution (Rasmussen 1977). However, it is unlikely that new salt marshes of a similar magnitude to those at present will develop. Firstly, most of the present salt marshes are situated along coasts backed by steep slopes, allowing less space for development of new marshes. Secondly, it is unlikely that the surrounding farming community will accept loss of agricultural land. Hence, one may expect a new coast line with shallow waters retaining *Zostera* beds adjacent to a much narrowed fringe of salt marshes barraged from the agricultural land. The climate scenarios with increased precipitation and more frequent storms would reduce productivity on the marshes, forcing the brent geese to switch to agricultural feeding during periods of high water levels. This scenario of future brent goose habitat availability and habitat use ought to be addressed in a more detailed analysis, covering not only the Agerø area, but all sites used by the Svalbard light-bellied brent goose population.

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tion of the model, together with an associated model of *Zostera* availability, is found in Clausen (1994).

During field work, it seemed that the use of the *Zostera* beds in spring coincided with periods of low water level, induced by easterly winds. The switch from salt marsh to fjord or vice versa was not a simple linear response, with flocks of brent geese gradually abandoning the salt marshes to feed on *Zostera* as the water level fell. Instead it appeared that brent geese showed a discrete switch response within a very narrow water level range. An approximate test of this on/off response was made by use of a logistic model:

$$y = \frac{1}{1 + \exp(c_1 \cdot (x - c_2))} \quad (\text{Eq. 1})$$

where y is the proportion of brent geese feeding on the fjord, x is the average daily water level (ADWL), c_1 and c_2 constants. Implicit in this model is that y develops asymptotically towards 1 for falling water level and towards 0 for rising water level. The constant c_2 equates to the water level at which half of the brent geese are found on the fjord, and hence hereafter is termed the 'switch' water level, because when $x = c_2$ then:

$$y = \frac{1}{1 + \exp(c_1 \cdot (c_2 - c_2))} \cdot \frac{1}{1 + \exp(0)} = 0.5 \quad (\text{Eq. 2})$$

The constant c_1 determines the slope of the curve.

Rearranging and applying the natural logarithm throughout Eq. 1 gives:

$$\ln\left(\frac{1}{y} - 1\right) = c_1 \cdot (x - c_2) = c_1 \cdot x - c_1 \cdot c_2 \quad (\text{Eq. 3})$$

This equation was used in an approximate test of the correlation between the ADWL and habitat choice, transforming the proportion of brent geese feeding on the fjord, y , to $\ln(1/y - 1)$. Tests were made for each year and spring period. Observations of all and none of the brent geese feeding on the fjord were taken as 0.9999 and 0.0001, respectively, because of the asymptotic requirements of the model. When the ADWL and the transformed proportion of brent geese feeding on the fjord were significantly correlated, the constants c_1 and c_2 were estimated from the transformed data by simple linear regression, and used in Eq. 1 when fitting the curves of habitat use

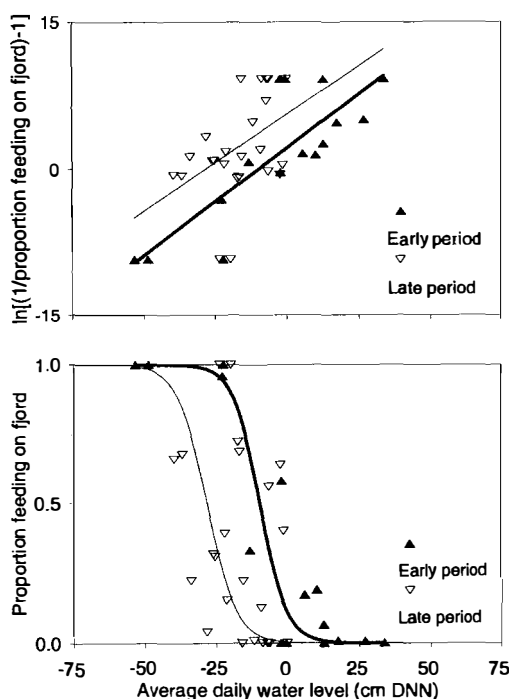
Appendix

Modelling effects of water level on habitat use

In the main text of this paper, reference is made to a model used to determine the water level at which the brent geese switch from feeding on subtidal *Zostera* beds to feeding on land. The full descrip-

Table A1. Linear regressions of the natural logarithm of the transformed proportion of brent geese feeding on the fjord ($1/y - 1$) in relation to the average daily water level, and parameter c_1 and c_2 estimates for early and late spring periods 1989–1993. None of the slopes was significantly different from the others. Intercepts, and thereby c_2 estimates, that were not statistically significantly different are given the same letter in the column to the right (Tukey q-tests, $P > 0.05$).

Period	Slope c_1	Intercept $-c_1 \cdot c_2$	N	Probability regression	Calculated "switch water level" c_2	Probability c_2
Early 1989	0.27	2.83	15	0.0003	-10.65	B D F
Early 1990	0.23	-1.80	16	0.0001	7.92	A C E G
Early 1991	0.42	6.65	8	0.0418	-15.80	B
Early 1992	0.38	-1.49	17	0.0001	3.89	A C F G
Early 1993	0.22	2.10	15	0.0002	-9.62	B D F G
Late 1989			17	0.7577		
Late 1990			16	0.7527		
Late 1991	0.36	-0.29	11	0.0001	0.82	A D F G
Late 1992	0.25	2.84	24	0.0001	-11.34	B D
Late 1993	0.21	5.78	25	0.0354	-28.15	B



in relation to ADWL (Fig. A1). Tests of equality of slopes, c_1 , and intercepts, $-c_1 \cdot c_2$, was made by multiple comparisons of linear regressions (Zar 1984) (Table A1).

Fig. A1. Modelled effects of water level on habitat use of brent geese, exemplified by data from spring 1993. The upper graph shows linear regressions between the natural logarithm of the transformed proportion of brent geese feeding on the fjord ($1/y - 1$) in relation to the average daily water level. The lower graph shows curves of habitat choice of brent geese in relation to the average daily water level, fitted by estimates of constants c_1 and c_2 derived from the regressions. Early spring period: 21 March–25 April (bold lines); late spring period: 26 April–31 May (thin lines).

Habitat use and site fidelity of Svalbard light-bellied brent geese *Branta bernicla hrota* at Lindisfarne: Exploitation of a novel food resource

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Percival, S. M. & Anderson, G. Q. A. 1998: Habitat use and site fidelity of Svalbard light-bellied brent geese *Branta bernicla hrota* at Lindisfarne: Exploitation of a novel food resource. Pp. 295–301 in Mehlum, F., Black, J.M. & Madsen, J. (eds.): Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skrifter* 200.

Light-bellied brent geese *Branta bernicla hrota* wintering at Lindisfarne moved from their traditional intertidal feeding grounds to feed on autumn-sown cereals in significant numbers for the first time in late December 1995. This was repeated in the following year. In both years the birds stayed 6–8 weeks longer than usual, with most departing in March rather than January/early February. This new food resource was available in greater abundance than the birds' usual food plants and, being especially rich in soluble protein, was also of higher nutritional quality. As it had not been utilised previously, factors other than food supply must have been restricting its use. Marked individuals showed a low return rate to cereals, suggesting further that the birds did not prefer to feed on this habitat. Birds using cereals arrived later at Lindisfarne and we suggest that their late arrival in poor condition after their mid-winter migration from Denmark may have contributed to their need to seek out novel food resources. Smaller numbers of dark-bellied brent geese at the site made less use of the cereals than the light-bellied sub-species. The move to feed on agricultural land has considerable implications for the conservation management of this goose population. Although providing the geese with an improved food supply at a time of year when alternatives are sparse, the move also has the potential of bringing them into conflict with agriculture. The provision of nutrient-rich alternative feeding areas may be a possible solution.

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Introduction

Until 1995, the Svalbard light-bellied brent goose population was one of the few European goose populations that had not moved to exploit agricultural land outside the breeding season (Madsen 1984; Clausen et al. 1998; Clausen & Percival 1998, this volume). We have been carrying out a study of these birds at their wintering grounds at Lindisfarne, NE England, studying their habitat use at both the population and the individual scale. In 1995/96 the geese showed a major change in behaviour, moving from feeding on intertidal habitats to feeding on autumn-sown cereals in significant numbers for the first time. Occasional records of up to 500 birds on cereals had been reported during the previous 30 years but these birds spent only a few days on this habitat before either leaving the site or moving back to their traditional areas (Smith 1977; D. O'Connor, pers. comm. and Percival and

Anderson unpubl. data). This paper documents that change, examines the resource availability in traditional and novel habitats and looks at which individuals have utilised this 'newly discovered' food resource.

In many other goose populations, such a move onto agricultural land has been coincident with substantial increases in numbers (Madsen 1991). Whilst reduced shooting mortality was likely to have been the most important factor driving these population changes (Ebbinge 1991), increased food availability was essential in supporting the expanding numbers. At the same time, this habitat switch has brought many of these populations into conflict with agriculture (Patterson et al. 1989; Summers 1990; Percival & Houston 1992). Such conflict at Lindisfarne could cause serious problems for the conservation of the brent goose population. An understanding of how and why the birds are utilising this novel food resource is therefore essential for effective management in the future.

Methods

Bird numbers

Complete counts of brent geese (in all the areas that they use at Lindisfarne) were carried out at least weekly from September to March in 1993/94, 1994/95, 1995/96 and 1996/97. The habitats on which each flock was found were also recorded. Where more than one count was made in a seven-day period, mean figures were used for that week. Counts of the two sub-species of brent geese occurring at Lindisfarne, *Branta bernicla hrota* and *B. b. bernicla*, were made to determine the proportions of each sub-species on the different habitats that they used, to test whether there were any differences in habitat use between them.

Habitat availability

The extent of brent goose feeding habitats at Lindisfarne was determined by ground survey of the intertidal mudflats and from 1:10,000 Ordnance Survey maps. As analysis of droppings collected at Lindisfarne has shown that brent geese on the salt marshes feed almost exclusively on *Puccinellia maritima* (Anderson 1998), the area of salt marsh dominated by *Puccinellia* was used as the available feeding area on this habitat. The area of winter cereals available was determined as the total area of all fields that were used during a season by the brent geese.

Food plant biomass and nutritional quality

Surveys of the mudflat vegetation were carried out in autumn and winter in 1994/95, 1995/96 and 1996/97 to determine the cover (and hence biomass density) of *Zostera* and *Enteromorpha* spp., following the methodology of Percival et al. (1996). The biomass density of *Puccinellia* on the salt marshes was determined in autumn and winter 1994/95 by measuring vegetation heights from 50 random plots. These measurements were converted to biomass using a calibration curve based on sample clipped plots. No account was taken of *Puccinellia* regrowth as this was unlikely to have

been an important factor at this site at this time of year (Rowcliffe et al. 1995; Anderson 1998). No direct measurements of the biomass density of the cereal crops were made.

Food plant and dropping samples were assayed for soluble protein (Read & Northcote 1981; Anderson et al. 1997) and water-soluble carbohydrates (Southgate 1976), using 8 replicates from each habitat. Samples were collected in early January 1997 when the birds moved on to the cereals. To avoid problems with the potential uptake or excretion of inorganic grit affecting the calculated concentrations of food components, all results have been expressed in terms of organic dry weight. The digestibility of different food components was calculated using an estimate of overall digestibility of the total food plant material. A mean value of 32% was taken from previous studies where the overall digestibility of graminoid or herbaceous plant material was determined for captive, adult brent geese in the non-breeding season (Boudewijn 1984; Lane 1994). Measurements of digestibility are often subject to error but such errors in this parameter make only a small contribution to the overall estimates of apparent digestibility (Anderson 1998). The term 'apparent digestibility' was used because the calculations do not take account of endogenous material excreted along with undigested food, although this material is generally assumed to have a negligible effect on digestibility calculations in birds (Karasov 1990). Apparent digestibility for each food component α was calculated using the equation:

$$\text{Apparent Digestibility}^{\alpha} (\%) = 100 \times (1 - \{(1 - 0.32) \times [(\text{percent } \alpha \text{ in faeces})/(\text{percent } \alpha \text{ in food})]\})$$

It was not possible to separate the components of the birds' droppings on the mudflats (*Zostera* and *Enteromorpha*), so a combined apparent digestibility was calculated.

Marked individuals

We had been catching brent geese using cannon-nets at Lindisfarne from January 1991 to March 1997. A total of 397, 332 light-bellied and 65 dark-bellied, were caught, with an additional 11 marked in Svalbard and 3 in Denmark during this period, all light-bellied. Only a single ringed dark-

bellied bird was seen on the cereals. It was excluded from all the analyses. All were given an individually coded engraved darvic plastic ring and individual colour-ring combination. The latter was important to extend the distance at which individuals could be identified up to 1 km. This was in particular essential on the mudflats.

All flocks were checked for rings during the weekly counts, and to ensure as complete and as even a coverage of the ringed birds as possible, additional supplementary visits were made regularly throughout the season to all the areas used by the brent geese.

Analysis of sightings data

An initial examination of cumulative frequency plots of the numbers of individuals observed through time each year was made to estimate resighting rates.

The overall pattern of site use at Lindisfarne was investigated by determining at which of the three main mudflat sites each individual was seen. This pattern was compared between each of the four years. Birds were excluded from this and subsequent analyses for the year during which they were caught so that the sample period would cover the entire year for all birds. Only a single bird from each family unit was included so that individuals were independent.

The return rate of individuals to Lindisfarne was calculated as the proportion of birds observed in one year that were also observed in the subsequent year. The return rate to cereals was calculated for 1995/96–1996/97 and compared with the return rate to Lindisfarne as a whole. To determine if there was any evidence of differences in arrival dates, first sighting dates of birds using cereals were compared with those not seen on this habitat.

Results

Bird counts and habitat use

Numbers and phenology of the brent geese were very similar for the first two years, when the birds did not make any significant use of autumn-sown

cereals (Fig. 1). The numbers built up gradually from September (week 1) to a peak count of just over 2500 birds in December (week 14, and then declined steadily so that very few birds remained by the end of February (week 26). In 1995/96 the build up of numbers and the size of the peak count were quite similar to previous years but the peak count was maintained for a much longer period. The decline began in February (week 20), two months later than in 1993/94 and 1994/95. In 1996/97, the phenology was again different, with the increase in numbers continuing well after the usual peak was reached in late December (week 15). A maximum of over 4000 was recorded in January (week 21), more than a month after the usual peak count. As in 1995/96, the main decline took place later than in previous years (from week 21). The use of the mudflat feeding grounds was similar between all four years. This habitat was used exclusively for feeding in the first part of the season (to week 10–18) but its use declined rapidly from then on. The use of salt marsh was also similar between the years, with a few hundred birds recorded in the latter part of the season. Birds usually began using the salt marshes only at high tide and then switched to using them through the whole tidal cycle. Autumn-sown cereals were used briefly by a small number of birds (up to 240) in 1993/94 (around weeks 20–22) but not at all in 1994/95. In 1995/96 the birds showed a major change, with up to 1250 birds feeding on cereals from the end of December (week 18) through to the end of March (week 30). The same behaviour was repeated in 1996/97, with a peak of 1750 on this habitat. A small number of birds used pastures for feeding in 1995/96 and 1996/97.

The ratio of dark-bellied:light-bellied brent geese was lower on the cereal fields than on the traditional habitats (saltmarsh and mudflats) in both 1995/96 (2.8% dark-bellied on cereals compared with 10.0% elsewhere: $\chi^2 = 274.3$, $p < 0.001$) and 1996/97 (1.4% dark-bellied on cereals compared with 5.2% elsewhere: $\chi^2 = 124.6$, $p < 0.001$).

Food availability and quality

The biomass densities of the three main components of the mudflat vegetation at the start of the season (early September) are shown in Table 1.

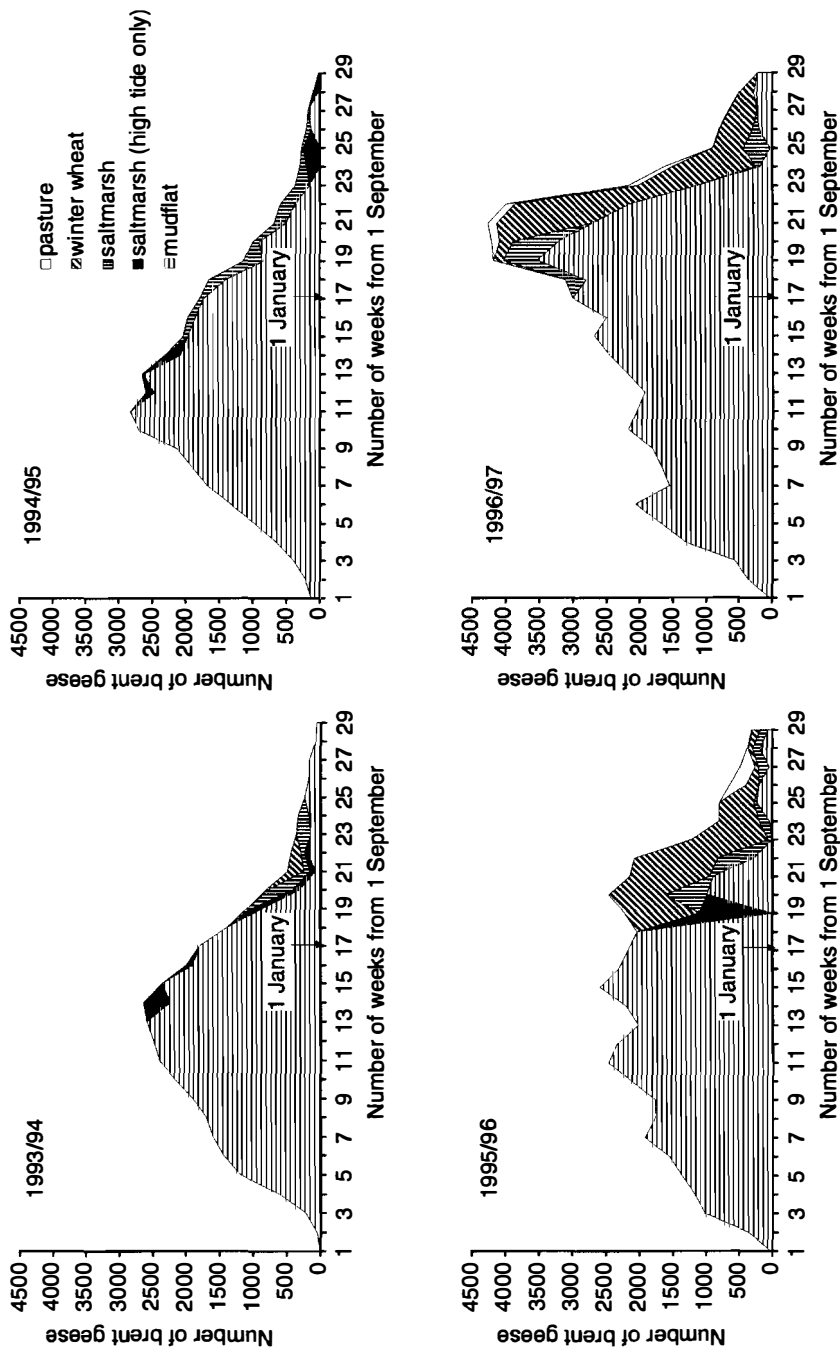


Fig. 1. Weekly brent goose counts and habitat use Lindisfame.

Table 1. Initial food plant biomass densities for 1994/95, 1995/96 and 1996/97. Figures are in g dry weight m⁻². Values for above-ground biomass are given for *Zostera* spp.

Plant species	1994/95	1995/96	1996/97
<i>Zostera noltii</i>	10.2	9.3	6.7
<i>Zostera angustifolia</i>	5.5	7.6	5.8
<i>Enteromorpha</i> spp.	33.2	27.6	15.1

There was little variation between 1994/95 and 1995/96, though the abundance of both *Zostera noltii* and *Enteromorpha* were both lower in 1996/97. Though *Enteromorpha* was initially more abundant, high non-grazing losses meant that it was a less abundant food resource than *Zostera* for much of the season (Percival et al. 1996). The mean *Puccinellia* biomass density at the start of the season was 97 gm⁻², but the total food resource was less as the area of saltmarsh was much less (41 ha compared with 625 ha of mudflat vegetation). By the end of December, when the move to cereals took place, biomass densities of the intertidal vegetation had declined to the threshold at which the birds could no longer satisfy their food requirement (Percival & Evans 1997). *Puccinellia* densities at that time were around 50% of their initial value. The area of autumn-sown cereals used in 1993/94, 1995/96 and 1996/97 was 37 ha, 120 ha and 140 ha respectively. No birds were seen using cereals in 1994/95.

The quality and digestibility of the different nutritional components of the mudflat vegetation, *Puccinellia*, and autumn-sown wheat are summarised in Table 2. *Zostera* was generally low in soluble protein, whilst the salt marsh vegetation was intermediate in protein but high in carbohydrate. The cereal (wheat) was very high in soluble protein but had the same carbohydrate content as the mudflat vegetation. Apparent digestibilities did not vary much between the plants tested, though protein digestibility was slightly lower in the mudflat vegetation.

Habitat use by marked individuals

Cumulative frequency plots showed 86–100% resighting rate during the 4 years. Thus the large majority of individuals were recorded each year. Both cereals and traditional habitats had an equally high resighting rate.

Table 2. Concentrations of soluble protein and water-soluble carbohydrates for plants from three habitats used by brent geese at Lindisfarne in January 1997, with apparent digestibility (AD) of each component. Concentrations are expressed as % of organic dry weight. Data are presented as means \pm 2SE.

Plant species	Soluble protein	Water-soluble carbohydrates
<i>Zostera noltii</i>	3.3 \pm 1.4 ^a	24.2 \pm 6.2 ^a
<i>Enteromorpha</i>	8.7 \pm 1.6 ^b	22.8 \pm 4.2 ^a
Apparent digestibility	84.5 \pm 8.2	79.1 \pm 12.6
<i>Puccinellia maritima</i>	9.6 \pm 0.8 ^b	35.6 \pm 4.2 ^b
Apparent digestibility	93.6 \pm 4.8	80.3 \pm 9.8
<i>Hordeum vulgare</i>	22.1 \pm 4.4 ^c	21.7 \pm 3.2 ^a
Apparent digestibility	95.5 \pm 7.8	79.8 \pm 11.0

^{a,b,c} For plant and dropping composition data: within a column, for each category (plants or digestibilities), values with different superscripts are significantly different (one-way ANOVA, $p < 0.001$, Tukey's multiple comparison tests, $p < 0.05$). Column categories without superscripts have no significant differences

The annual return rate to Lindisfarne (i.e. the percentage of birds seen there in one year that were also seen there in the following year) was 66%, 74% and 70% ($n = 79, 76$ and 103) in 1993/94, 1994/95, and 1995/96, respectively. A total of 20 and 46 individuals were recorded feeding on cereals in 1995/96 and 1996/97 respectively. This represents 26% and 37% of the marked individuals recorded at Lindisfarne for each year respectively. Of those 20 in 1995/96, only 7 (35%) were seen back on cereals the following year. Of the remaining birds, 2 did not return to Lindisfarne and the other 11 (55%) returned but were not seen on cereals.

Birds using cereals had a significantly later first observation date than those that were not seen on this habitat. The median first date for individuals that used cereals was 10 January in 1995/96 and 14 January in 1996/97. The equivalent dates for birds that were not seen on cereals were 23 October and 2 December. This difference was statistically significant in both years (Mann-Whitney $U = 358$, $p = 0.016$ in 1995/96 and $U = 814$, $p < 0.001$ in 1996/97).

Discussion

In late December 1995 a major change took place in the feeding site selection of the Svalbard

population of light-bellied brent geese wintering at Lindisfarne. Birds moved across the sea wall to feed on autumn-sown cereals in significant numbers for the first time. They also extended their stay at the site, with most birds leaving in late February/March rather than early January/February.

The cereals provided the geese with a high quality food resource, being rich in soluble protein content (a readily assimilated source of nitrogen, Anderson et al. 1997). The amount of this new food source was also considerably greater than either the mudflat or salt marsh vegetation. At this time of year biomass densities of the winter cereals would be about the same as the salt marsh (Patterson et al. 1989; Summers 1990; McKay et al. 1994) but the cereals extended over a greater area. Both salt marsh and cereals would have been at much higher biomass density than the intertidal vegetation. Thus, both in terms of food quality and food quantity the geese benefited by moving on to the cereals. However, given the depletion of the intertidal vegetation (Percival & Evans 1997) through the season, the question remains as to why this switch to cereals had not taken place (a) earlier in the year and (b) in other years. In both 1995/96 and 1996/97 the switch to cereals coincided with a period of freezing air temperatures when alternative food supplies on the salt marshes were unavailable (as they were covered by frost and ice). As most of the food on the mudflats had been depleted by this time, this was the only available food source then. Thus it appears that even though the cereals provided an abundant high quality food resource, the geese only used it when they had no other alternative food source. Until then the birds seemed reluctant to fly over the sea wall to use this habitat. Once their feeding pattern on this new resource was established, however, the geese continued to feed there for the remainder of the season until their migration to their spring staging grounds in Denmark. Their reluctance to fly across the sea wall may be influenced by disturbance (or at least the birds' perception of disturbance/predation risk) which may have been influencing the use of these habitats, as it does on the mudflats (Percival et al. 1996). The local farmers did frequently scare the geese from the cereal fields. In addition, as most of the hunting on the site takes place along the shore, the geese would have to cross a key shooting zone in order to reach the cereal fields.

There was no evidence that the dark-bellied

sub-species, which feeds regularly on cereal crops in other parts of its wintering range (Summers 1990), was the main species involved in the move on to cereals. Indeed the brent flocks on the cereals had a lower proportion of this sub-species than the traditional mudflat and salt-marsh habitats.

The behaviour of individually marked brent geese supported the hypothesis that cereals were not a preferred habitat. Only a third of the birds using the cereals in 1995/96 returned to them in 1996/97, compared with a return rate to the site overall of 70%. However, considering the generally small samples in this analysis, the results should be viewed with caution. First observation dates suggested that birds using the cereals tended to arrive later at Lindisfarne than those not using them. These later arrivals may have been in poorer condition, having been forced to move across the North Sea to Lindisfarne by ice winters in Denmark in both years. They may have been in such a nutrient deficit that they had to feed on the nutritionally better habitat despite a higher risk of disturbance/predation.

The switch to feeding on agricultural land could have considerable implications for the conservation management of this population. Agricultural land provides the birds with improved food availability but it can also bring them into conflict with local farmers. Shooting to reduce agricultural damage is not acceptable because the population is so small, so the management options are limited. Provision of high quality, low disturbance alternative feeding areas (Owen 1990) may provide the best long-term solution if the geese continue to feed on farmland. It is clear that the birds' use of Lindisfarne, both in terms of phenology and habitat selection, is dynamic, and that there is both spatial and temporal complexity in the way in which the site is exploited by the geese. Further studies are ongoing to investigate the consequences of cereal use for the birds' survival and reproductive rates. In addition, development of the feeding site selection models for the geese on their traditional habitats (Percival et al. 1996) to include this new food supply should facilitate our understanding of the birds' use of these alternative feeding habitats.

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Changing trade-offs between predation risk and food intake: Gaining access to feeding patches during spring-fattening in pink-footed geese *Anser brachyrhynchus*

JESPER MADSEN



Madsen, J. 1998: Changing trade-offs between predation risk and food intake: Gaining access to feeding patches during spring-fattening in pink-footed geese *Anser brachyrhynchus*. Pp. 303–311 in Mehlum, F., Black, J.M. & Madsen, J. (eds.): Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skrifter* 200.

During spring staging in western Jutland, Denmark, pink-footed geese feed in large open fields. In more northerly stopover sites in Vesterålen, northern Norway, fields are small. Compared to western Jutland, geese in Vesterålen were more tolerant to human activity and in Vesterålen, herons and gulls did not elicit escape flight as frequently as in western Jutland. During mid-May in Vesterålen, light conditions allowed geese to feed throughout the 24-hour cycle. During daytime, geese fed in outer fields farthest away from human settlements and roads. At night, when the level of disturbance from human activity was least, geese fed intensively; progressively during May, they exploited field zones close to roads and lawns in gardens and between buildings. The risk-taking behaviour was adopted instantaneously on arrival in Vesterålen, suggesting that compared to western Jutland geese in Vesterålen made a different trade-off between predation risk and food intake, which enabled them to increase the use of patches which would otherwise have been unavailable. These behavioural adjustments are important for the acquisition of body reserves prior to nesting.

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Introduction

From experimental and observational studies there is evidence that a foraging animal possesses the ability to assess the risk of being preyed upon and to incorporate this information into its decision making of when, where and how to feed (see review by Lima & Dill 1990). Thus, avoidance of risk of predation may strongly influence patch use. However, if, for example, an animal is in high demand of food intake, it may be willing to run a higher risk of predation and enter 'dangerous' patches to feed.

Prior to migrating to the breeding grounds, arctic-nesting geese accumulate body nutrient and energy stores which are prerequisites to successful reproduction (Ankney & MacInnes 1978; Ebbinge et al. 1982; Thomas 1983). Several studies have emphasised the importance of favourable feeding conditions in the spring staging areas for the acquisition of body stores, focussing on food plant quality and energy intake rates (e.g. Ydenberg & Prins 1981; Boudewijn 1984; Madsen 1985a; Prop

1991; Prop & Deerenberg 1991). However, very little attention has been paid to the role of behavioural trade-offs made by geese to meet the high energy and nutrient demands.

In the population of pink-footed geese *Anser brachyrhynchus*, which breeds in Svalbard and winters in Denmark, The Netherlands and Belgium, spring-fattening starts in staging areas in western Jutland, Denmark. From late April to mid-May, the geese migrate to staging areas in Trondheimsfjorden in central Norway and in Vesterålen and Lofoten in northern Norway. During their stay in Norway, the geese accelerate spring-fattening by feeding on the first grass growth which is of high nutritive quality (Madsen et al. 1997; Madsen unpubl.). They thus achieve peak condition prior to their final departure towards the breeding grounds around 20 May (Madsen 1994; Madsen et al. 1997). This paper illuminates another factor which contributes to the rapid fattening process, namely behavioural change which can greatly enhance feeding opportunities.

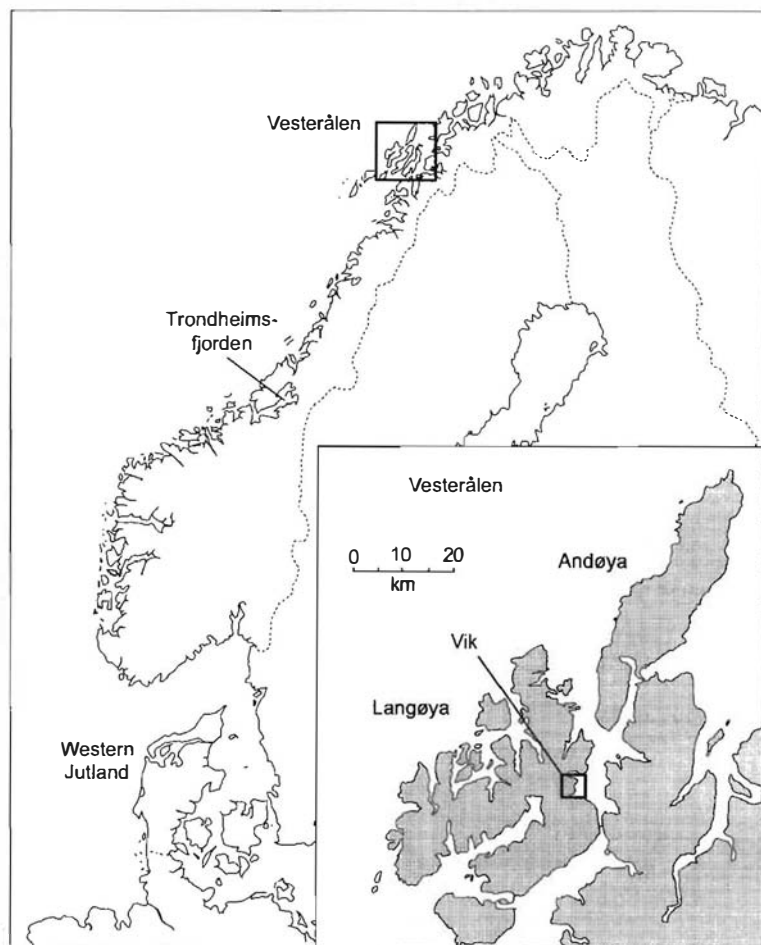


Fig. 1. The spring staging areas of pink-footed geese and the Vik study area in Vesterålen (insert).

Study area

Field studies were carried out in the Vik area on Langøya, Vesterålen in northern Norway (Fig. 1) during May of 1991 (pilot study), 1992 (main field season) and 1993. This area is one of the most important spring staging areas for pink-footed geese in northern Norway, supporting approximately 2500 geese during mid-May (B. Røsshag unpubl.). Due to the northerly location, there is never complete darkness in May. During mid-May, the sun sets around 22 hrs and rises before 02 hrs.

The geese feed mainly in lowland pasture fields close to the coast, and they roost on the coast

nearby. The pastures are used for sheep and cattle grazing as well as for hay cutting. Fields are composed of a mixture of *Agrostis tenuis*, *Poa pratensis*, *Phleum pratense* and *Festuca pratensis*, with colonisation of *Deschampsia caespitosa* in older fields. Pastures are reseeded at 4–6 year intervals. The size of the fields used by the geese ranges from less than 1 ha to approximately 10 ha, with a median width of <100 m. In comparison, fields used by pink-footed geese in western Jutland have a minimum width of approximately 600 m (Madsen 1985b).

From 6 to 20 May, 1992, air temperatures measured at Vik (Vågønes Research Station, unpubl. data) ranged from -4 to 14°C , with a mean daily average of 3.3°C .

The white-tailed eagle *Haliaeetus albicilla* is abundant in Vesterålen and an infrequent winter visitor in western Jutland; it is known to be a natural predator of pink-footed geese in northern Norway (B. Røsshag pers. comm.; Madsen unpubl.). Grey herons *Ardea cinerea* and large gull species flying over goose flocks elicit increased vigilance or escape flight. Herons, herring gulls *Larus argentatus* and great black-backed gulls *Larus marinus* are common in both western Jutland and northern Norway.

Methods

Diurnal activity budgets of randomly selected goose flocks were described by instantaneous recording of the numbers of individuals engaged in different activities (rest, graze, walk, alertness, swim, fly, interact, preen) at quarter-hourly intervals (Altmann 1974). From 9 to 14 May 1992, most hours in the 24-hour cycle were covered twice.

All anthropogenic or natural stimuli eliciting increased vigilance or escape flight were recorded. In the instance of escape flight, the distance from the stimulus to the nearest edge of the flock before taking flight was visually estimated to the nearest 5 m. For comparison, similar observations were carried out in western Jutland, Denmark, during the spring of 1982–1984 (Madsen 1985b) and 1991–1993. Because escape flight distances increase with flock size (Madsen 1985b) and may vary according to habitat type, only data on small flock sizes (20–100 individuals, the most frequent flock sizes in Vesterålen) and on pasture feeding flocks were used for comparison.

Twice each day (between 10 and 16 hrs) and twice each night (between 22 and 06 hrs) during 10–19 May, 1992, the number of geese in the study area was counted by use of binoculars or a telescope from a car, and the position of the flocks was mapped on a 1:5000 scale map. For analysis, a grid (100 m × 100 m) was superimposed on the field maps, and assuming that there was an even distribution of birds within the flocks, numbers were apportioned between grid cells. The number of bird-days per grid unit was calculated for daytime (defined as 08–20 hrs) and nighttime (20–08 hrs), respectively.

To estimate the consumption rate of the above-ground standing crop of the pasture vegetation by geese, an enclosure experiment was carried out. In two pastures in Vik, paired sets of exclosed and grazed plots were erected on 7 May 1992. Both pastures had been reseeded 3–4 years earlier, were southfacing, and were dominated by *Poa pratensis*. In each pasture, five sets of plots were established, with a paired plot at 50 m intervals along a transect perpendicular to a road, starting 10 m from the road or a farm building adjacent to the road. Each enclosure (40 cm × 40 cm) was defined by four 50 cm high corner pegs; wires at three elevations and diagonal wires at the top prevented geese from entering the enclosures. In exclosures and grazed plots the green biomass was measured on 7, 13 and 19 May. In a 50 cm² plot inside each enclosure and in the grazed sward two m away from the enclosure and marked with a peg at ground level, the length of all green shoots of all grass plants was measured with a ruler to the nearest mm. Shoots of varying lengths were collected, dried and weighed to establish a relationship between shoot length and weight. The standing crop was calculated as g dry weight per m².

To estimate the length of stay of individuals in the study area, neck-banded geese were recorded 3–4 times daily during 7–19 May 1992 by the author, and before and after that period by local observers. Pink-footed geese have been banded with blue neckbands with a three-digit code engraved in western Jutland since 1990 (Madsen et al. 1997). Neckbands can be read with a telescope at a distance of up to 700–1000 m. In 1991–1993, approximately 1% of the population was marked with neckbands. The length of stay of an individual was calculated as the number of days from first to last observation. A pair of neck-banded geese was recorded as a single unit, i.e. only one of the birds was used in the calculations.

Between-year rate of return to the study area by individually marked birds was calculated for birds observed there in one year and known to be alive in the subsequent spring. The re-sighting probability of individuals during April–May was approximately 99% (Madsen & Noer 1996). The rate of return was calculated for 1991–1992 and 1992–1993. The day-to-day resighting probability of individuals in Vik was 0.67, 0.82 and 0.70 in 1991, 1992 and 1993 (Madsen unpubl.).

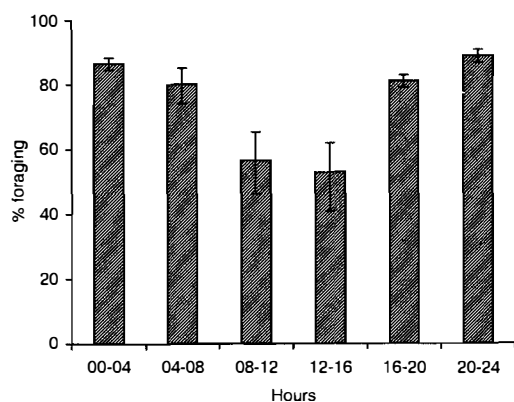


Fig. 2. Diurnal foraging activity of pink-footed geese in Vesterålen, May 1992, expressed by the hourly proportion of individuals engaged in foraging, averaged in four-hour blocks (arc-sine transformed means \pm S.D.).

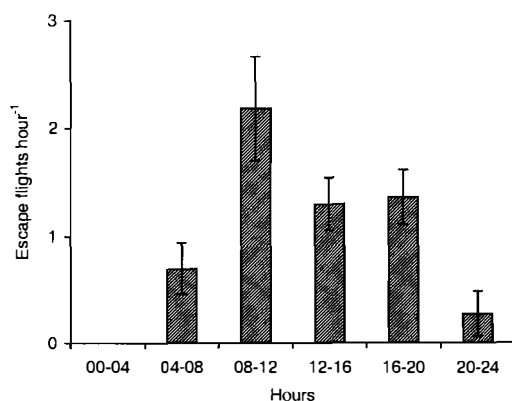


Fig. 3. Diurnal variation in the rate of disturbance of flocks of pink-footed geese in Vesterålen, May 1992, expressed by the number of escape flights observed per hour, averaged in four-hour blocks (\pm S.D.).

Results

Diurnal activity budget

Pink-footed geese fed throughout the 24-hour cycle, with peak activity during night and a drop in activity during daytime (Fig. 2). On average (weighed in 4 hour blocks), a goose spent 74% (17½ hours) of the 24 hour cycle feeding. The drop in activity during daytime was related to increased human activity and, consequently, more frequent disturbance of the flocks (Fig. 3). Depending on the source of disturbance, flocks flew short distances to land in the fields again to resume feeding, or they flew to the coast to roost, preen or swim before returning to the fields to feed.

Reaction to human activity and natural predators

When flying grey herons passed flocks of pink-footed geese in western Jutland, they elicited escape flight in 90% of the observed cases; in Vesterålen herons elicited escape flight in 26% of the observed cases (Table 1). When large gull species overflowed goose flocks, geese flew up in 32% of the observed cases in western Jutland versus in none of the observed cases in Vesterålen. In both areas, the geese took flight in all observed cases when white-tailed eagles flew overhead.

In western Jutland, pink-footed goose flocks took flight at a distance of on average 133 m when approached by car; in Vesterålen, flocks took flight at an average distance of 17 m (Table 2,

Table 1. Frequency of escape flight reaction by flocks of pink-footed geese to overflying potential predators and their 'look-alikes' in western Jutland and northern Norway, respectively.

	White-tailed eagle			Grey heron ^a			Large gull ^b		
	Escape	Stay	% escape	Escape	Stay	% escape	Escape	Stay	% escape
W Jutland	2	0	(100)	18	2	90	6	13	32
N Norway	14	0	100	5	14	26	0	9	0

a: the difference between western Jutland and northern Norway is highly significant ($\chi^2 = 13.81$, $P < 0.001$; with a Yates' correction); b: the difference between western Jutland and northern Norway is highly significant ($\chi^2 = 19.85$, $P < 0.001$; with a Yates' correction).



Fig. 4. Pink-footed geese crossing the main road on Langøya, Vesterålen, May 1992. Photo: J. Madsen.

Table 2. Escape flight distance by pasture feeding flocks (20–100 individuals) of pink-footed geese to approaching cars in western Jutland and northern Norway, respectively.

	Mean (m) ^a	S.D.	n
W Jutland	133	75	23
N Norway	17	6	16

a: the difference between western Jutland and northern Norway is highly significant (Student's *t*-test, $t = 7.38$, $P < 0.001$).

Fig. 4). The escape flight distance did not change during 7–19 May 1992 in Vesterålen (Spearman rank correlation, $r_s = 0.192$, $n = 16$, $P > 0.05$).

Numbers and patch use

Due to immigration and emigration as well as local movements, numbers in the Vik area fluctuated from day to day. During daytime, the pink-footed geese in Vik concentrated in the fields furthest away from roads and buildings, referred to as 'distant zones'; at night they aggregated in field zones close to roads and buildings, referred to as 'close zones' (Fig. 5). At night, flocks of geese were observed feeding on grass lawns in gardens and between trees.

The change from the distant field zones to the zones close to roads and buildings was gradual. Hence, during 8–12 May, the geese almost exclusively used the distant zones both day and night. From then onwards, an increasing number

started to use the close zones at night, whereas during daytime, numbers only slowly increased, peaking on 19 May (Fig. 6).

Length of stay and rate of return

The length of stay of individuals in Vik ranged from 1 to 18 days (Fig. 7). Mean length of stay was 4.3 days. However, neckbanded geese observed only once were likely to be transients on their way to another staging area in Vesterålen; if this category of birds was excluded, the mean length of stay was 6.3 days.

Of 29 individuals observed in Vik in 1991 and known to be alive in 1992, 11 were observed again in 1992 (37.9%). Of 63 individuals observed in 1992, 20 were observed to return in 1993 (31.8%). There was no significant difference between years ($\chi^2 = 0.12$, $df = 1$, $P > 0.05$), and combined, the rate of return was 33.7%. There was no significant difference in rate of return by adult males, adult females and juveniles (the two sexes combined) ($\chi^2 = 1.08$, $df = 2$, $P > 0.05$).

Exploitation of pasture vegetation

On 7 May, there was no significant difference in standing crop within exclosures in the two study fields (Student's *t*-test, $t = 0.87$, $P > 0.05$). Data from the two fields were therefore pooled. From 7 to 19 May, the standing crop in the exclosures increased from an average of 11.4 ± 2.7 (S.D.) to

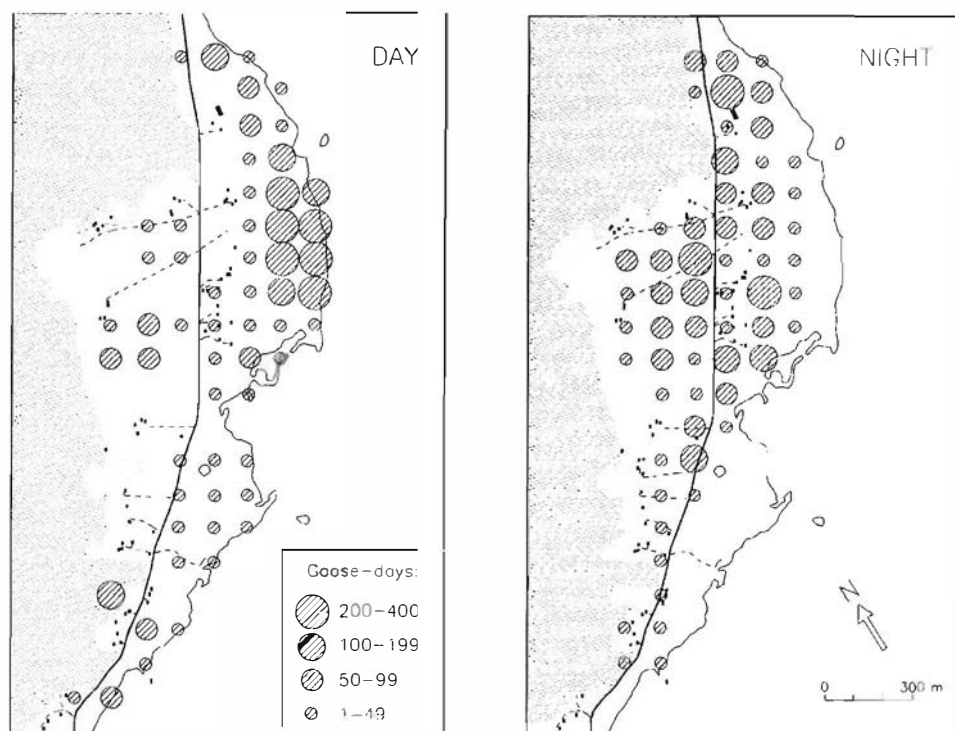


Fig. 5. Diurnal distribution of pink-footed geese in the Vik area, Vesterålen, May 1992. The number of goose-days is calculated per 100 m \times 100 m grid cells. Stippled areas: hill/mire/wood; bold lines: road; stippled lines: lane; dots: buildings.

15.7 ± 2.8 g dwt m^{-2} . In grazed plots, the standing crop decreased from 9.2 ± 2.6 to 6.3 ± 3.4 g dwt m^{-2} . In plots within 100 m from roads and buildings, the vegetation was untouched by the geese on 13 May, while heavily grazed in more distant plots. On 19 May, all plots had been grazed, showing a gradient in grazing pressure from the roads/buildings to the distant plots (Fig. 8).

Discussion

During their stay in northern Norway, the pink-footed geese are time-stressed to build up body reserves prior to migration to the breeding grounds, and they feed intensively throughout most of the 24-hour cycle. However, the available feeding sites are small and the biomass of food is low, although high in quality. In comparison, the green standing crop in similar types of pastures in

Denmark during mid May is 10-fold that in Vesterålen (Lorenzen & Madsen 1985). There is evidence to suggest that in most spring seasons the Vesterålen staging area is almost filled to capacity with geese (Madsen unpubl.).

This study shows that the geese adapt behaviourally to the local environment and the time-stress. Firstly, in becoming more tolerant to human activity (which is perceived as a potential predator, see also Gill et al. 1996), the geese are able to exploit more of the resources in the feeding patches. If the geese had maintained the wariness towards humans as observed in western Jutland, most of the fields in Vesterålen would be unsuitable for foraging because of their small sizes. Secondly, the 24-hour feeding opportunity makes it possible for the geese to feed uninterruptedly at night when human activity is at a minimum; they can thereby invade patches which are not accessible during daytime. Thirdly, discriminating more carefully between natural potential avian predators (eagles) and their 'look-alikes' (herons and gulls, which are not natural

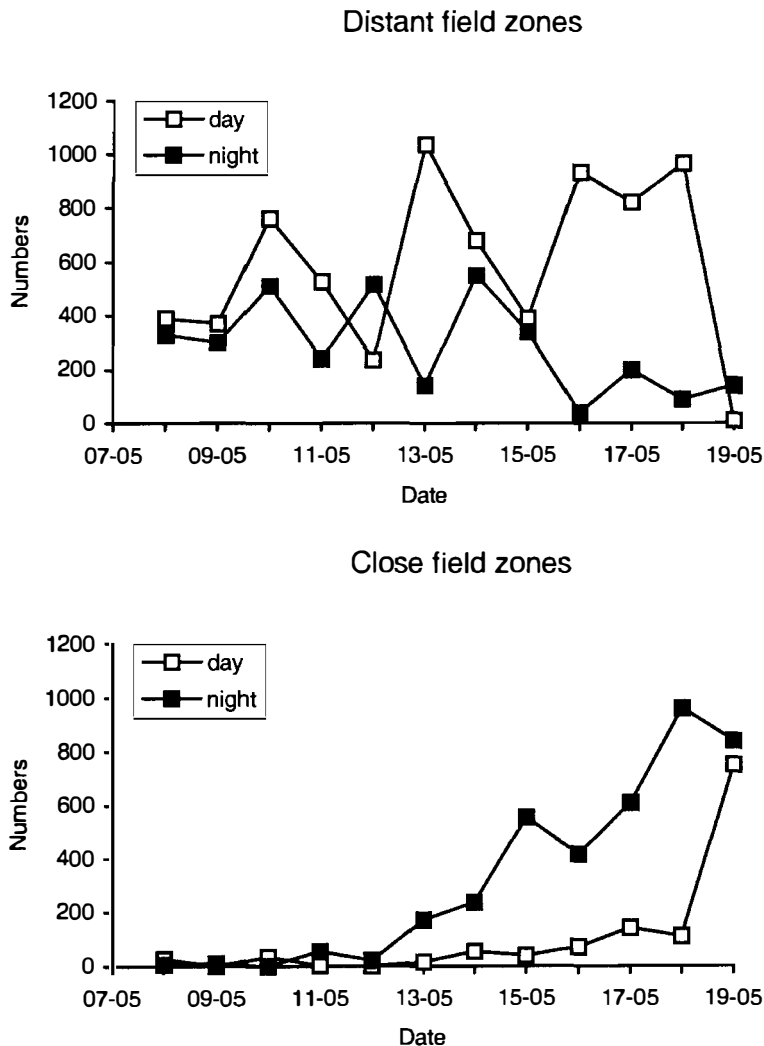


Fig. 6. Diurnal numbers of pink-footed geese in distant fields zones (>100 m away from roads and buildings) and field zones close to (≤ 100 m) roads and buildings, Vik, May 1992.

predators of pink-footed geese but may be perceived as such because they resemble eagles), the geese avoid losing important feeding time and spend less energy due to flying which is very costly in terms of energetics.

Risk-taking behaviour was adopted instantaneously on arrival in Vesterålen. This indicates that, based on previous experience with the area, geese made a decision to compromise safety rather than habituate gradually to the environment. Although some geese stayed for more than two weeks, the majority of geese stayed in the study area for a relatively short period, which limits the time available to habituate. Approximately one-third of the marked individuals

returned to the study area, and more than 80% of the marked individuals returned to Vesterålen in general (Madsen unpubl.). So even if the degree of site-fidelity to the specific site is moderate, it is possible that long-lived species such as the pink-footed goose have a capacity for learning patch qualities and risks of the general area.

The observed increasing use of the field zones close to roads and buildings can be explained either by a change in trade-off between predation risk and intake rates as the resources in the distant fields become depleted or by habituation. Again, because of the turnover of individuals, the latter explanation is unlikely.

Why do the geese not make similar trade-offs

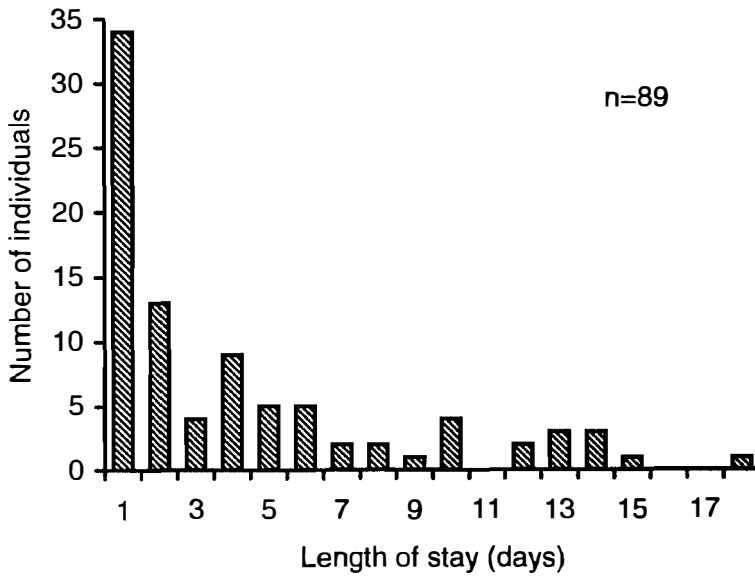


Fig. 7. Length of stay of individually marked pink-footed geese in the Vik area, May 1992.

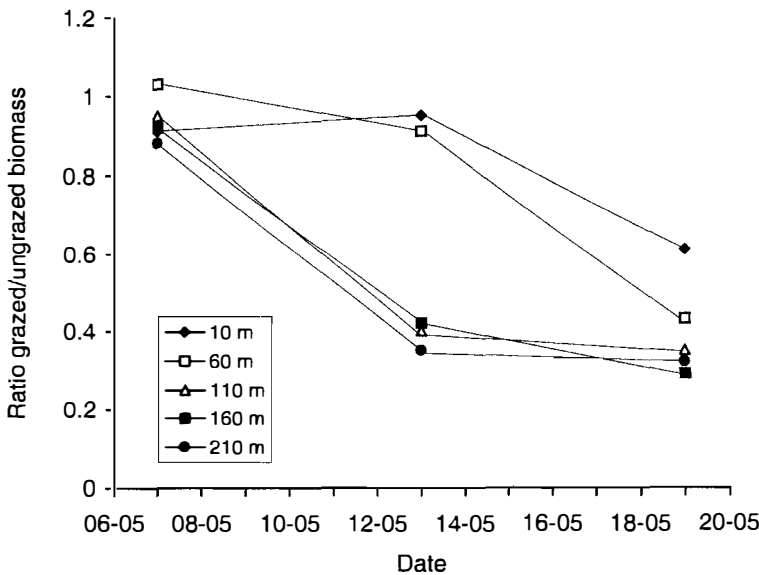


Fig. 8. Grazing pressure exerted by pink-footed geese in pasture plots at varying distance from roads/building in the Vik area, May 1992. Grazing pressure is expressed by the ratio between grazed and ungrazed (exclosed) standing crop (g dwt m^{-2}) in paired plots on three sampling dates. Each dot represents two sets of paired plots.

during their stay in western Jutland? An explanation might be that there is more 'slack' in the time and energy budget there (Madsen 1985a) and, consequently, the geese do not have to run similar risks of predation. Furthermore, in western Jutland, flocks of geese are frequently scared away from newly sown fields by farmers (using various scaring devices including shotguns) and

therefore generally wary when approached by humans.

To conclude, the utilisation of Vesterålen as a staging area for pink-footed geese would be extremely limited if the geese did not behaviourally change the trade-off between the risk of predation and food intake. The risk-taking behaviour enables the geese to expand patch use as

well as reduce energetically costly activities. Because available space and time are limited, the changes in behaviour are important for the acquisition of body stores prior to reproduction.

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Arctic geese: Herbivore-vegetation interaction, predators and human pressures—a symposium synthesis

RUDOLF H. DRENT and FRIDTJOF MEHLUM



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A symposium on the Svalbard geese was hosted by the Norwegian Polar Institute in Oslo, Norway, 23–26 September 1997, to collaborate new information on the three goose populations that breed in Svalbard: the barnacle goose *Branta leucopsis*, the light-bellied brent goose *Branta bernicla hrota* and the pink-footed goose *Anser brachyrhynchus*. This paper attempts to synthesise information gained in recent years on these goose populations. Also echoed here are management problems related to these goose populations and priorities for future research.

Looking back over several decades of intensive effort devoted to the goose species breeding in Svalbard, four research themes are touched upon. We argue that (A) unravelling the mechanisms of response of the individual to increasing population density is both technically feasible and theoretically rewarding. A cooperative effort here deserves unflagging priority if we are to achieve population models useful for management purposes. Although individual responses at the various sites utilised through the annual cycle fit the paradigm of density dependence, this does not imply overall population control. The weakest link in the causal chain is (B) understanding the interaction between geese and their food plants, and we contend that this topic should head the new research agenda. This work can profitably be linked with (C) new technologies which allow the tracking of individuals in relation to potential food supplies that can in turn be quantified by means of remote sensing techniques. Under ideal conditions the birds can subsequently be recaptured and profiles of past energetic expenditure reconstructed from indwelling heart-rate loggers. Finally, the geese are not alone, and (D) various predators (notably arctic foxes, polar bears and man) have major impacts on habitat use and influence goose numbers both directly and indirectly, often in an interaction with weather conditions (ice and snow cover). Recently there have been major changes in numbers and distribution of these key predators and at least locally they may now be acting to limit goose populations.

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The density dependence paradigm

For many years the main thrust of avian population studies was to confirm the existence of density dependence (by experiment if possible). Most of the work related to breeding output, clutch size being the best-worked feature. Although by no means universal, the reality of density-dependent checks on breeding is now indisputable (Newton 1998). This allows us to move on to examine the proximate mechanisms that lead to demographic adjustment (for example change in clutch size) and the selective advantage that accrues to the individual that 'obeys the rules' embodied in the density-dependent relationships. From the viewpoint of population management, it is vital to persevere in the study of populations exempt from human hunting pressure until the chain of density-dependent processes at each stage of the annual cycle has been modelled with enough confidence to allow prediction.

Long-term waterfowl studies have similarly revealed the reality of density-dependent effects on reproductive output, and the snow goose studies can serve as our crown witness. Drawing on a massive twenty-year data base on the lesser snow goose *Anser caerulescens caerulescens*, Cooke et al. (1995) noted in their study colony on the Hudson Bay lowland that a long-term decline in clutch size, nesting success, pre-fledgling gosling survival and immature survival have accompanied the overall increase in adult numbers. These changes relate to a decline in food availability in the major salt-marsh feeding areas, reflecting degradation in both the extent and quality of forage available. During the last two decades, survival of the adult breeders has in fact increased, so we are faced with the paradox of conditions conducive to high adult survival and low reproductive output. Habitat degradation in the colony area does not merely reflect a local increase in the nesting goose population, but its extent is directly

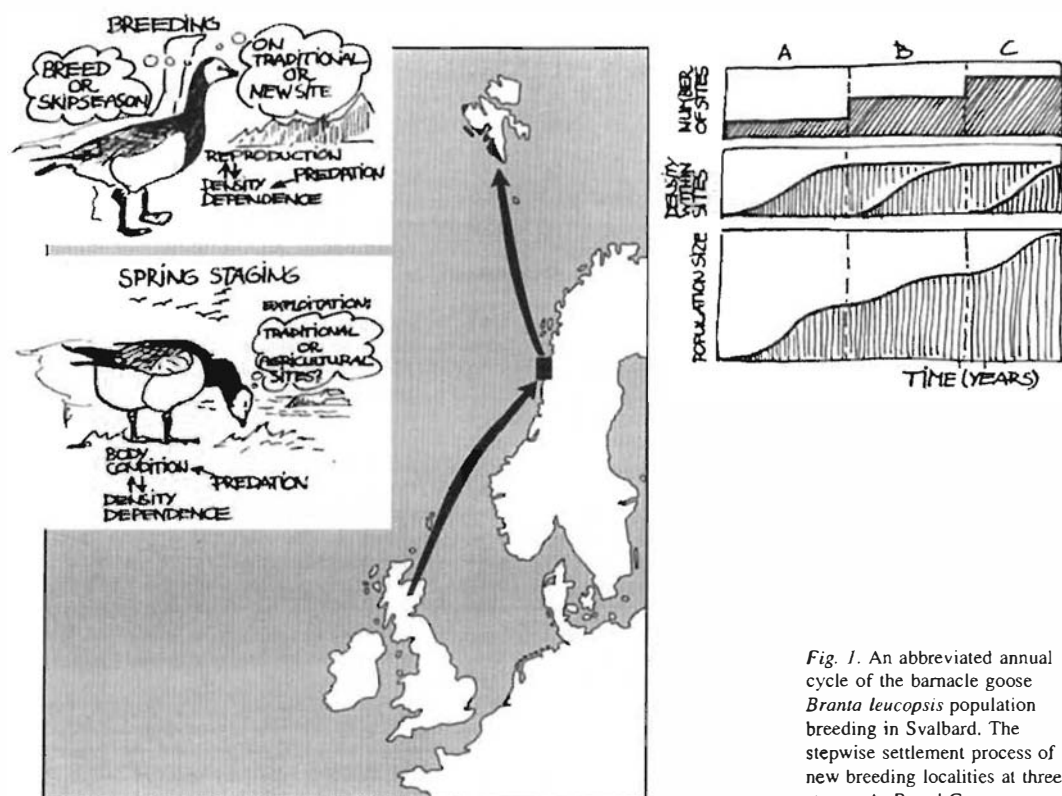


Fig. 1. An abbreviated annual cycle of the barnacle goose *Branta leucopsis* population breeding in Svalbard. The stepwise settlement process of new breeding localities at three stages, A, B and C.

influenced by destructive 'grubbing' activities when geese extract rhizomes from the soil upon arrival in early spring. Many of the birds using the site at that time are in fact passing through on their way further north, and the imbalance between the birds and their breeding habitat reflects the escape of the snow goose population as a whole from the set of checks and balances formerly acting outside the breeding season in the wintering and staging grounds further south. The resulting mismatch is responsible for extensive damage to the salt marsh vegetation of the Low Arctic (Jefferies 1988), not only in the La Pérouse study area but over a widening arc of localities (Jano et al. 1998).

This dramatic demographic upset has engendered a drastic policy shift in North America regarding hunting. Aside from the management problem, the lesser snow goose study underlines the message that in the case of migratory populations, growth of numbers under the vastly increased carrying capacity of the wintering grounds (abundance of suitable agricultural crops) is not necessarily brought under control by density-dependent reductions in reproductive out-

put on the breeding grounds. We must remember that density-dependent mechanisms themselves evolve under the pressure of natural selection on individuals and do not by definition lead quickly to some tidy balance sheet of stable numbers.

The Svalbard barnacle goose

For the barnacle goose *Branta leucopsis*, an abbreviated annual cycle is here depicted and will serve as a frame of reference (Fig. 1). The concentration of the Svalbard barnacle goose in winter and the well-defined spring staging and breeding range provide ideal opportunities for study of population processes (Mehlum 1998, this volume). The gradual, if somewhat piecemeal, accumulation of evidence linking wintering and summering ranges dates from Boyd's (1961) pioneering demonstration that the barnacle goose population with which we are concerned is a separate entity (judiciously deduced from ringing recoveries and the aerial survey of the wintering population 1959/60). Commencing with the spring

staging areas along the Norwegian coast just below the Arctic Circle, we have seen (Prop & Black 1998, this volume) that the choice facing the incoming migrants is to choose between the traditional sites and the more developed, modern agricultural alternatives. This choice is exacerbated by the simultaneous pressures of an increasing goose population coinciding with a deterioration of foraging habitat in the traditional sites due to the progressive abandonment of sheep grazing on the outer islands. Presumably the strong site faithfulness of the experienced individuals reflects the selective advantage of retaining control over choice foraging sites familiar from previous years, but this conservative system can only be maintained if adequate performance is guaranteed in succeeding years. This is one of the features incorporated in the spring staging model (Lang et al. 1998, this volume). Subsequent breeding performance will depend in large part on attainment of adequate body condition. To what extent individual pairs achieve this is liable to reflect a compromise between accepting either the intensive strife at well-visited traditional sites (including frequent disturbance by predators such as sea eagles) or the shift to the new agricultural areas. Prop & Black point to the qualitative differences in the nature of the body reserves accumulated at the alternative feeding sites. The leading question is whether in fact the new alternatives characterised by a lower rate of accumulation of body protein are not in fact a poor second choice, despite the enhanced opportunities for deposition of fat. This point deserves redoubled attention as the data to hand from the spring staging areas offer the tantalising suggestion of a qualitative gate limiting reproductive performance.

Events on the breeding grounds involve a number of choices with a superficial resemblance to events at the staging areas. The choice of the summering (and moulting) site in the first summer visit to the breeding grounds as adolescent pre-breeder is liable to impinge on a whole succession of subsequent life history decisions. The future mate is most likely selected from the members of the non-breeding flock which the young bird joins for the summer (Choudhury & Black 1994; Black 1998a, this volume) and prospecting in the local breeding colonies may determine the goal for the next summer. Unfortunately, we do not have access to a rich set of case histories to discern patterns in this phase of intertwined choices, but

the evidence to date points to the overriding influence of these early decisions on rates of change in the population as a whole. The first summer appears to be a sort of apprenticeship and represents an exploratory phase which is doubtless under the influence of density-dependence, helping to define for example foraging performance. Recruitment to the breeding colony remains a mysterious process, but we do know that once the individual has bred, the probability is high that it will be faithful to the site.

The overall settlement pattern is visualised as a stepwise process (Fig. 1) where suitable new breeding stations are colonised as a chance process, a few individuals becoming founders of new colonies (Mehlum 1998, this volume). Subsequently the new colony area absorbs increasing numbers (both by accepting immigrants as well as recruitment of young born locally) for some time until levelling off. Taking events along the Nordenskiöldkysten as indicative, local capacity of the summer range for the barnacle goose is limited by the interaction between safe foraging areas (principally lake margins) and predator pressure (nowadays mainly arctic fox *Alopex lagopus*) during the annual moult of the flight feathers (Drent et al. 1998, this volume). The parents (at that time accompanied by their small goslings) are restricted in their habitat use by their extreme vulnerability to predation, and competitive interactions determine which individuals gain access to the limited grazing sites. Foraging grounds are thus a more likely candidate for local population limitation than nesting sites (Tombre et al. 1998, this volume; Mitchell et al. 1998, this volume).

Events at this time cast their shadows ahead because the interplay between predator pressure, forage quality and quantity, and the number of families with which the resource must be shared, set the growth conditions for the goslings (see Loonen et al. in press; Loonen et al. 1998, this volume; Stahl & Loonen 1998, this volume). Not only is early growth vital to ensure survival during the veritable marathon of the fall migratory journey, but since eventual adult body size is also determined at this time, early growth conditions may play an important role in defining performance in later life (through the intermediary of dominance). There must be some competitive filter which the non-breeders (the failed parents and sub-adult hopefuls) must pass through at this time, even though their choice of feeding site

during the flightless period is skewed more towards marginal but safer zones than in the case for families. Provisionally, birds of the various social classes have been lumped together, but obviously more detailed knowledge will be needed to interpret pressures leading to return or emigration and to ascertain if indeed events during the moult play a crucial role in influencing the decision of the next year.

With the increasing number of barnacle geese, declines in both gosling production (Drent et al. 1998, this volume) and adult body size (Black et al. 1998, this volume) have been documented for the intensive study areas, reminiscent of findings in the lesser snow geese. One of the major revelations of our symposium was that these density-dependent effects are locally based (confirming Owen & Black 1989a; Owen & Black 1991) and that they tend to become submerged in a population-wide survey. Taking the data as a whole, the resultant mix of old colony areas (with declining production and growth rate) and new colony areas (temporarily at least released from density-dependent checks) makes it difficult to discern the underlying population processes (Pettifor et al. 1998, this volume). Large inter-annual variation in predator pressure on the breeding grounds further complicates the picture, resulting in highly variable gosling production (Loonen et al. 1998, this volume) not only by direct depredation but also by lowered survival perspectives of the remaining goslings herded together at high density in the relatively predator-safe areas (Stahl & Loonen 1998, this volume). Variable weather conditions in the Arctic (particularly the date of snowmelt, Prop & de Vries 1993) often intervene to mask the underlying density dependence in reproduction. It is comforting to find so many parallels in the reality of density-dependent features in reproduction of the Gotland population of the barnacle goose (Larsson & van der Jeugd 1998, this volume) established in the Baltic as an offshoot of the Russian stock.

Putting migration on the map

Until recently, study of the actual migratory journey linking the areas exploited by the geese at various seasons was a story of inference from before-and-after comparisons attesting to the hazards of the fall migration (Owen & Black 1989b). The implementation of satellite tracking

now provides individual migratory trajectories in geese (light-bellied brent geese *Branta bernicla hrota*; Gudmundsson et al. 1995; Clausen & Bustnes 1998, this volume). The findings by Clausen & Bustnes that the light-bellied brent geese breeding in northern Greenland and Svalbard are linked contradict the traditional view that the Greenland birds are linked to the population from Arctic Canada which winter in Ireland. This new information calls for a reassessment of the conservation strategies for the light-bellied brent geese in Europe. In the barnacle goose these devices have been combined with heart rate telemetry culminating in the realisation of the ecologist's dream in providing a record of energetic expenditure en route (Butler & Woakes 1998, this volume). The success of this needle-in-haystack procedure entailing the recapture of the individuals the year after to retrieve the implanted heart rate loggers attests to the unique opportunities provided by the research facility at Ny-Ålesund.

Striving for generality

Let it be thought that the exigencies of research in the Arctic have prevented us from reaching a satisfactory understanding of the chain of decisions facing the individual up to the time of first nesting, let us turn to the study of the marked shelduck *Tadorna tadorna* population pursued at the Ythan Estuary breeding locality in Scotland by Patterson and his team for upwards of twenty-five years (Patterson 1982; Patterson et al. 1983). The sequence of recruitment to the breeding population in the shelduck consists of progressing through a competitive series of hoops. First, the young bird must compete to enter the non-territorial flock associated with a breeding station. Next, pair formation and territorial behaviour provide access to the breeding population, which at the Ythan study area showed a remarkable stability through two decades of counts. An analysis of population parameters revealed that this stability of the territorial component could only be explained by some density-dependent process limiting entry, most likely in relation to the food resources of the defended site (paired females enjoy exclusive feeding rights during the pre-laying, laying and incubation phase). Patterson speculates that flock size of the non-territorial pool is also limited by competition for resources (such as food or space).

As is the case for geese, density-dependent effects limit hatching and fledging success in the shelduck. Overall, then, the general scheme of events resembles the nested decisions we have adduced for the barnacle goose, but in neither case do we have sufficient data to construct a pathway model quantitatively.

The frustration that disappointed the Patterson team of not being able to balance the local population budget without recourse to immigration (which could not be quantified satisfactorily, particularly with regard to the male sex) is a feature of the barnacle goose study as well. We now realise that detailed observational records at a number of colony areas at the level of detail achieved by Tombre et al. (1998, this volume) for the Kongsfjorden area will be needed to understand relations between them, acting as they do as communicating chambers. The arctic environment has impressed all of us working there with the reality of *extrinsic* controls (notably weather directly and through its impact on the vegetation, and predators) on population processes, and the time has come to dissect the *intrinsic* controls to achieve a quantitative understanding of how competition translates into numbers.

Our new research agenda

Uniting as it did the interests of management and conservation as summarised by Black (1998b, this volume) and Bø et al. (1998, this volume), the agenda served to identify areas where redoubled efforts are needed to satisfy current research demands. In particular, the question was raised if sufficient effort is being devoted to the herbivore-vegetation interaction on the long-term and large scale required to provide early warning of impending change. The rather fragmentary evidence so far from Nordenskiöldkysten points to a redistribution of foraging geese rather than vegetation degradation during the local population rise. There are functional explanations for the lack of a 'trophic cascade effect' engendered by goose grazing on the Spitsbergen range (Loonen & Solheim 1998, this volume). This rather slim line of evidence is congruent with the conclusions on goose-vegetation interactions from the high arctic study of the increasing greater snow goose *A. c. atlantica* population on Bylot Island, Canada (Manseau & Gauthier 1993; Hughes et al. 1994a; Hughes et al. 1994b). These observations reassure

us that a major upset on the breeding grounds as witnessed for the lesser snow geese is not imminent (see Abraham et al. 1997) and reaffirms the urgent need for an on-going monitoring effort on the arctic range including vegetation, goose grazing and the interaction with reindeer grazing.

The limited availability of *Zostera*

A suite of papers (Clausen 1998, this volume; Clausen & Percival 1998, this volume; Percival & Anderson 1998, this volume) deal with the behaviour and habitat use of light-bellied brent geese at their wintering sites in Denmark and England. The studies indicate that the *Zostera* beds in the subtidal zone are the preferred feeding areas compared to the adjacent and less productive salt-marshes. It is also suggested that the geese spend less energy as a reaction to disturbance in the *Zostera* beds compared to the other feeding habitats. Water level conditions may restrict the availability of *Zostera* beds, and the geese switch to salt marshes and agricultural land when *Zostera* is scarce.

The diminishing availability of *Zostera* is thought to be the major cause of the shift in winter habitat use by the light-bellied brent geese. The *Zostera* beds have decreased in extent or even disappeared at traditional wintering sites. Also the available *Zostera* beds have been depleted more rapidly during the season due to an increased goose population and by competition with other waterfowl. The cessation of grazing and hay cutting in salt marshes have probably also contributed to make salt marshes less attractive to the geese at some wintering sites. Light-bellied brent geese have recently started using a novel food resource, autumn-sown cereals, as alternative food when the availability of *Zostera* and salt marshes were limited. These changes in habitat use and potential conflicts with agriculture have to be addressed in the management of this goose population.

Population regulation in brent geese

In recent years much information on the Svalbard light-bellied brent population has accumulated. Despite some gaps in the knowledge, we know the locations of its main breeding, wintering and

staging habitats. It is also possible to pinpoint the key resource requirements for survival and fitness-maximisation in these habits. There is still a lack of data on reproductive rates in different parts of its breeding distribution range. However, it is likely that the reproductive rate of the birds breeding at Tusenøyane is a major determinant of the overall population breeding output (Madsen et al. 1998, this volume). Madsen et al. showed that predation, mainly by polar bear *Ursus maritimus*, is a limiting factor in the reproductive success of brent geese at Tusenøyane, and as this factor depends heavily on the seasonal conditions of the sea ice, it is highly erratic. The stochastic character of this predation makes it difficult to construct a predictive population model for management purposes and recalls the uncertainties that have beset modellers of the dark-bellied brent goose *B. b. bennicla* so far.

Behavioural plasticity in pink-footed geese

Most of the recent research on the Svalbard pink-footed goose *Anser brachyrhynchus* population has been conducted by the National Environmental Research Institute in Denmark and collaborators. This research has included a neck-banding programme (started in 1990) and has focused on individual variation in dispersion, migratory strategies and effects on body condition, survival and breeding success. Among the objectives are (1) looking at the effects of hunting on the population (survival impacts), (2) investigating body condition enhancement and migratory strategies at spring staging areas in northern Norway and their effects on fecundity, and (3) examine the influence of stress factors on winter body condition and survival. An important result of this research is that individual variation in migratory strategies, including site-faithfulness at the spring-staging areas in northern Norway, can be documented in terms of fitness-costs. Madsen (1998, this volume) demonstrated nicely the behavioural plasticity of these birds at their spring-staging areas as a trade-off between predation risk and food intake rate. Such behavioural adjustments have allowed the geese to modify migratory routes (and phenology) and even occupy new staging areas, so far without major conflicts with agricultural interests.

Bearing in mind that this is the largest of the three Svalbard goose populations and also the only population subjected to legal hunting, an extension of the research effort seems called for to keep one step ahead of management problems. Recent work has been mainly undertaken outside the breeding season, and consideration should be given to selecting a target area for summer work somewhere in the Svalbard archipelago. We have seen how useful such local studies have been in lending a focus to the work on the other goose species, but admittedly pink-footed geese are by far the most shy and require particularly circumspect methods on the breeding grounds.

Concluding remarks

Conferences tend to close with glowing accounts of future perspectives, and it is a sobering experience to read again Malcolm Ogilvie's masterful summary (Ogilvie 1984) of our previous gathering (1983) and compare the research agenda sketched there with what has actually been achieved. The paramount importance of study of the individual in order to achieve a causal understanding of the processes underlying population dynamics was sounded at that time, stressing the need to trace recruitment of offspring of the focal animals. Unfortunately the accumulation of pedigrees allowing fitness calculations has not kept pace with these vistas, and although we can describe skewness in reproductive performance, we have not yet gained insight as to how this comes about. Again, although the call for more research effort regarding habitat use and habitat selection has been followed through on the spring staging sites in Norway, this has not yet resulted in wider efforts which combine field surveys with the sophisticated remote sensing techniques now available (Jano et al. 1998). The third major thrust from the 1983 meeting was to intensify work on the staging areas and actual travel routes employed during the fall migration, and this work is off to a tantalising start thanks to technological innovation.

We all certainly endorse the view that long-term studies of geese are essential both for applied and theoretical reasons, as argued by Owen & Black (1991), and operationalised by Lang et al. (1998, this volume) as well as by Rowcliffe et al. (1998, this volume). These long-term studies provide the

only road to knowledge of changes in numbers likely in the future. We echo their challenge that '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 relates to its food resources.'

Acknowledgements. – The cooperative spirit engendered by the joint efforts of an international team under the umbrella of Norsk Polarinstitutt holds promise for the future. We dedicate this contribution to Hugh Boyd, our guide and mentor, in the hope that even in the absence of his editorial touch he will recognise some of the themes he has been developing through the years with his special olympian flavour.

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