The spring range of barnacle geese *Branta leucopsis* in relation to changes in land management and climate

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Abstract

This study examines recent changes in the distribution of spring staging barnacle geese *Branta leucopsis* in Norway. From the early 1980s onwards, two major changes have taken place. First, increasing numbers of geese moved from the traditional islands with a semi-natural vegetation towards agricultural fields on larger islands close to the mainland. Secondly, geese expanded their range by exploring more northerly located islands. Data on food exploitation by geese on the traditional islands were collected to interpret these changes. The density of shoots of edible grasses explained the spatial variation in grazing pressure over the traditional islands. This pattern was caused by intensive grazing of available habitat, where apparently a lower threshold of the intake rate set a limit to the amount of food cropped. It is concluded that the carrying capacity of the traditional islands had been reached. On many of the traditional islands, capacity declined, however, as the vegetation type with the highest density of grasses and most preferred by geese disappeared. This negative development seems to have started when people abandoned the islands and summer grazing by sheep stopped. The declining number of geese that can find sufficient food within the traditional range, in conjunction with the rapidly growing size of the total population, are the main causes for the observed expansion of the population. Increasing spring temperatures and a change in agriculture may have allowed the geese to move to the north, and to invade agricultural areas. To lessen conflicts between geese and farmers on the large islands, two lines of management are available: restoration of management on islands within the traditional range, and enhancing the attractiveness to geese of saltmarshes on the larger islands. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Branta leucopsis; Carrying capacity; Management; Climate change

1. Introduction

During the last few decades, many of the western Palaearctic goose populations have increased in numbers (Madsen, 1991) due to improved food conditions in winter (Owen and Black, 1991) and a decrease of hunting pressure (Ebbinge, 1991). Larger numbers of geese require more food and space, and this leads progressively to conflicts with agricultural interests (Owen, 1980; Groot Bruinderink, 1989; Madsen, 1992). To alleviate such conflicts, reserves have been created to attract geese away from vulnerable agricultural crops (Owen, 1980, 1990). Spring is a particularly critical period for potential conflicts, because this is when geese must accumulate body reserves needed for migration, and may achieve this by feeding on young crops that are also valuable for farmers.

The barnacle goose *Branta leucopsis* population breeding at Svalbard has enjoyed a period of rapid growth in numbers. In 1948, numbers were critically low, estimated at only 400 (Owen and Norderhaug, 1977), but the population currently exceeds 13 000 (Owen and Black, 1991). In the wintering area, this population seems to be safeguarded by the creation of the Caerlaverock refuge in Scotland (Owen, 1980; Owen et al., 1987). However, during spring migration the geese reside for several weeks on islands off the coast of Norway, and little is known about the numbers this area can sustain. When the population was smaller, geese used only the sparsely populated islets 30–40 km off the coast (Gullestad et al., 1984), but during the 1980s an increasing number settled some 15 km from the mainland on larger islands where agricultural practice is

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the mainstay for about a dozen farming families (Black et al., 1991). Local authorities were concerned that the geese would soon cross the sea and invade the larger-scale farming community on the mainland. Black et al. (1991) argued that the geese were attracted to the new area because the rich food supplies on the discovered fields surpassed the feeding opportunities in the traditional areas. Alternatively, the shift in distribution could have been induced by limited supplies of food on the traditional islands, leaving the growing numbers of geese no choice but to explore new areas. Perhaps this trend was enhanced by deteriorating foraging conditions on the traditional islands after the mass emigration of people from the islands in the 1970s; the local people used to manage the islands by cutting hay and grazing with sheep and cattle.

In this paper we review recent changes in numbers and distribution of the geese throughout the spring staging area and focus on the question of how many geese the traditional islands can sustain.

2. Study area

Data were collected on the Helgeland archipelagoes (centred at 65°45′N, 12°E) in Norway (Fig. 1). Many of the islands are flat and close to sea level, providing vegetation suitable for the geese. Each archipelago consists of several 'Home islands', with houses and barns, surrounded by a scatter of 'Outer islands'. Outer islands are not inhabited, but, traditionally, cattle and sheep were taken there in summer for periods of grazing. The main study sites were located on Sandvaer (1990), and on Laanan (1991, 1992). Permanent habitation of Laanan came to an end in 1979, which meant the end of a centuries-old grazing tradition (Gullestad et al., 1984). Since then sheep have been reintroduced for short periods (Black et al., 1991). Sandvaer is still home to c. 50 people, and some of the Home and Outer islands are managed in a traditional way (with 12–20 sheep). Our study area on the two archipelagoes comprised about half of the Home islands and several of the neighbouring Outer islands, totalling 25 ha in the Laanan group and 30 ha on Sandvaer. Geese stay in the area from the end of April to the third week of May. The main agricultural island used by geese is Herøy.

3. Methods

3.1. Goose counts

Annual counts were made at each archipelago in May from two or three of the highest vantage points in order to scan all the islands. Additional areas were counted from a small boat. Sometimes this process was made easier when white-tailed eagles *Haliaeetus albicilla* flew over and caused whole flocks to take to the air. Weather conditions prevented us from visiting all the islands each year. The number of geese on the islands that were not counted in a particular year were estimated by a loglinear model based on the actual observations in which the expected counts were a function of an island effect and a year effect (Pannekoek and van Strien, 1994; Underhill and Prys-Jones, 1994). On average, 17% of the total numbers were calculated in this way. The size of the total population was derived from counts in the wintering area (Black and Shimmings, unpublished).

3.2. Climatic trends

Temperature data for the months of April and May were available from five weather stations throughout the region (Det Norske Meteorologiske Institutt, monthly reports). Data were available for 1975–1992, the whole of the period over which goose data were
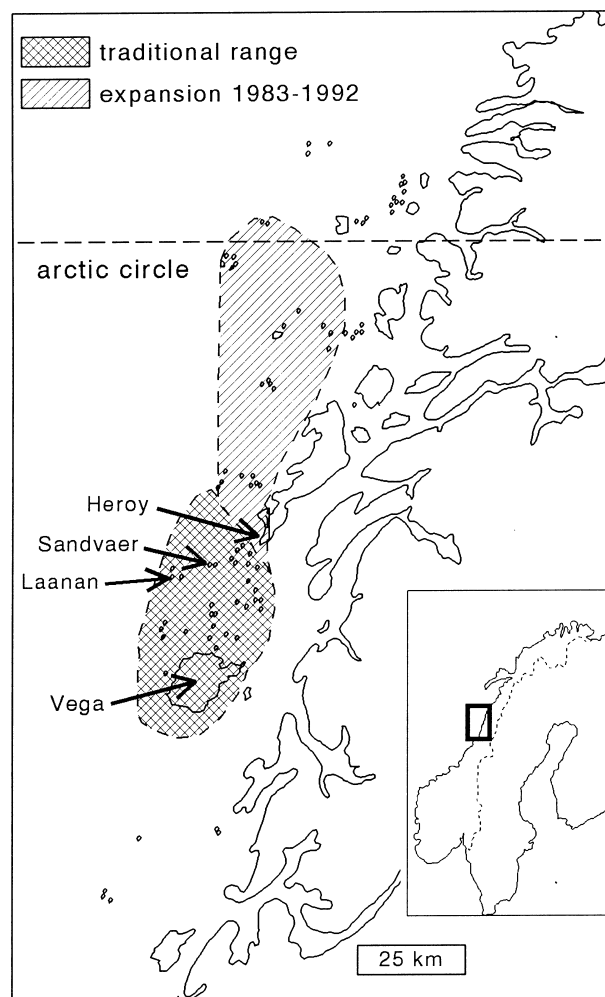

Fig. 1. The spring staging area of barnacle geese in Norway showing the traditional range (after Gullestad et al., 1984), and changes after 1983. No staging sites are known outside the area indicated.

collected. Since grasses show a continual turnover in leaves, where net grass growth (gross production minus death rate) is positive above c. 6°C (Peacock, 1975; Keatinge et al., 1979), the sum of positive temperatures at or above this figure was also examined for Vega (65°38′N, 11°52′E), an island within the spring range of barnacle geese where more detailed data were available (J. Antonsen, pers. comm.).

3.3. Dropping counts

Grazing pressure by geese was assessed by dropping densities (Owen, 1971). Permanent plots ($4 m^2$) c. 20 m apart were inconspicuously marked, and arranged in transects across the islands, or along the seashore. Droppings counted were removed at intervals of 1–3 days, and summed over the whole period of goose presence. In further analyses, plots were grouped per archipelago, year, island type (Home or Outer), and vegetation type (see below). To stabilize variances, statistical tests were performed on square root-transformed densities. Additional data on dropping densities were used from 1981 (Laanan), which had been collected in the same manner as in other years.

3.4. Vegetation analysis

In each of the plots used for dropping counts, the cover of grasses, herbs, mosses, dead plants and bare soil was visually estimated to the nearest 5% in May. Plots were compared in all combinations of pairs to obtain a matrix of dissimilarities (Whittaker, 1967). This matrix was used to group the plots into vegetation types by cluster analysis using average linkage between groups (Westhoff and Van der Maarel, 1978). To map the vegetation, boundaries of the vegetation types were drawn on topographical maps of the area (scale 1:2500) with an estimated accuracy well within 5 m. Maps were later digitized to calculate the area occupied by each of the vegetation types. In some of the plots, the density of grass shoots (or tillers) was estimated by counting the number of shoots in five randomly selected samples ($25 cm^2$ each) on the vegetated parts. The average density for each plot, as a measure of food availability, was calculated by correcting the shoot counts for the amount of bare area in the plot.

3.5. Intake rate and availability of food

The intake rate (IR) was calculated following Prop and Deerenberg (1991):

$$IR = PF \times LT \times NL \times W$$

where *PF* is the peck frequency, estimated by recording the time needed for 50 pecks by geese feeding in the immediate vicinity of the study plots and calculating the number of pecks per min; *LT* is the average leaf size taken in mm (derived from marked shoots, see below); *NL* is the number of leaves taken per peck, derived from close inspection of the sward to distinguish separate bites; this method was verified by close-up film records of geese feeding in small plots (Prop and Loonen, 1989); *W* is the dry weight of leaf per unit length, derived from measuring the lengths of leaves collected and subsequent drying to constant weight.

Festuca rubra and *Poa* spp. were the main food species in the study area (Black et al., 1991). To determine how much of the leaf was taken by geese, study sites were established: for *Festuca*, three on Laanan and one on Sandvaer; for *Poa*, two sites on both archipelagoes. At each site, one to three plots (20×40 cm) were inconspicuously marked. Within each plot, 24 shoots were marked with tiny plastic rings. The leaves of all shoots were measured to the nearest mm at intervals of 4 days, but more often when geese had visited the plots. This frequent sampling allowed matching of individual leaves between successive measurements. For each of the leaves, growth was calculated as the increment in length, or amount grazed as the decrement in length. Because in the species studied growth was restricted to one single (youngest) visible leaf (Prop, unpublished; Davies, 1981), the amount of grazing was corrected for growth as determined from other ungrazed blades.

To estimate food availability independently of the measurements on intake rate, 50 shoots were collected from each site on each date of sampling. The lengths of all green leaves were measured and summed per shoot.

4. Results

4.1. Change in distribution

In the 1980s, the number of geese in the archipelagoes abandoned by people (between 65°30′ and 66°00′ northern latitude) declined from > 3000 to < 1000 (Fig. 2). This decrease was partly compensated for by an increase in numbers in archipelagoes that were still traditionally managed (from c. 3000 in the early 1980s to 4000 in 1992). For example, one of the largest flocks of geese was found at Hysvaer where c. 60 sheep were kept during the winter months and 150 in the summer, and geese numbers have fluctuated between 1000 and 2000. Much of the growth in the goose population after 1982 was accommodated by the agricultural area of Herøy and Tenna, where from 1989 numbers stabilized at 3000. From 1988 onwards, geese also appeared to colonize islands to the north (Fig. 1).

The expansion of geese towards the north has coincided with a general trend towards warmer April and May temperatures in the region ($F_{1,84} = 5.44$, $p < 0.05$).
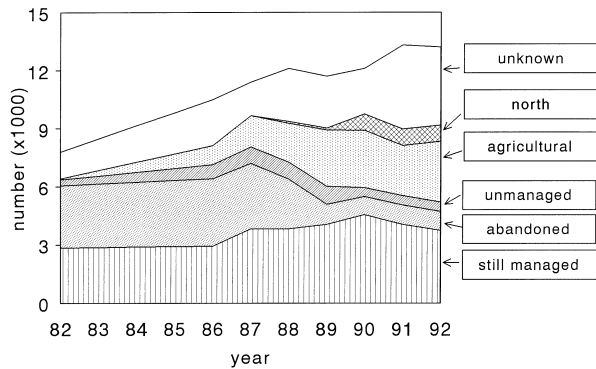
Fig. 2. Numbers of barnacle geese in Helgeland, Norway, grouped by management or location of the staging islands. The lower three groups represent geese within the traditional range. The discrepancy between the total population and the number of birds recovered in Norway is indicated by 'unknown'.

Although the annual increase in average temperature was only 0.04°C, the number of days with a temperature at or above 6°C has increased markedly by c. 50% throughout the years of study (Fig. 3).

4.2. Vegetation types

Cluster analysis of vegetation plots resulted in the following main vegetation types on the islands (Table 1):

(a) *Puccinellia*-meadows: occurring on sites which were inundated during spring tides. Total vegetation cover was c. 64%.
(b) *Festuca*-meadows: these formed the most prominent seashore vegetation in the study area. In May, dead leaves of *Festuca rubra* usually formed a dense layer.
(c) Moss-heaths: characterized by an extensive cover of *Drepanocladus* spp. and other moss species with a low density of graminoids (*F. rubra*, *Poa*
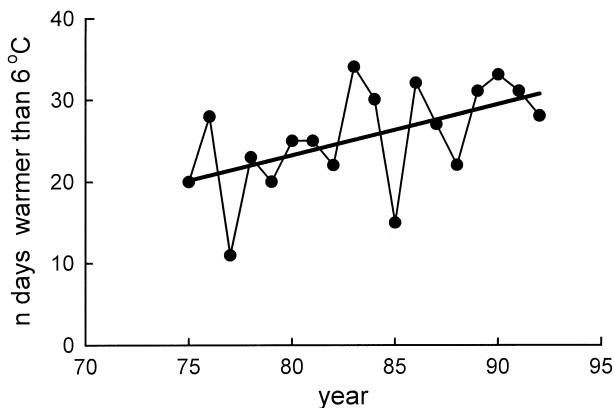

Fig. 3. The number of days in April and May warmer than 6°C during the years of study. Data from Vega, located in the centre of the traditional spring staging range ($y = 0.62x - 26.1$, $n = 18$, $r^2 = 0.27$, $p < 0.05$).

pratensis, *P. trivialis* and *Carex* spp.) and patches of *Juniperus communis*.
(d) Hay-meadows or pastures: dense sward of *F. rubra*, *P. pratensis*, *P. trivialis*, *P. annua*, *Agrostis stolonifera* and *Anthoxanthum odoratum*.
(e) Herb-meadows: areas with relatively extensive cover of herbs (mainly *Alchemilla* spp. and *Filipendula ulmaria*), and variable densities of grasses (mainly *Poa* spp. and *Anthoxanthum odoratum*).

The latter three communities covered the higher parts of the islands, and varied with changes in management. Hay-meadows occurred on islands that were used for stock. After management ceased on Laanan, the community transformed into herb-meadows (Table 2). Likewise, moss-heaths became herb-meadows after a plague of voles *Arvicola terrestris* in 1987 (Black et al., 1991) as they stripped the above-ground vegetation and 'ploughed' the soil.

4.3. Grazing pressure and intake rates

Grazing pressure (measured by the cumulative density of droppings over the season, Table 3) varied widely among vegetation types ($F_{4,367} = 6.00$, $p < 0.001$), being highest on *Festuca*-, *Puccinellia*- and hay-meadows and lower on herb-meadows and moss-heaths. There were no differences in densities between Home and Outer islands ($F_{1,367} = 0.28$, $p > 0.05$). Dropping densities varied among years ($F_{2,367} = 3.00$, $p = 0.05$), but the significant interaction term between year and vegetation type ($F_{5,367} = 5.01$, $p < 0.001$) indicated that this variation depended on the type of vegetation. One-way ANOVA for each vegetation type separately showed that annual variation occurred only in herb-meadows and moss-heaths.

The density of grass shoots, as a measure of food production, was determined for the *Festuca*-, herb- and moss-meadows. The cumulative number of droppings per plot appeared to be positively related to shoot density (Fig. 4), but there was no additional vegetation effect (ANCOVA with shoot density as covariate and year and vegetation type as factors; vegetation-term: $F_{2,160} = 0.24$, $p > 0.05$). This means that differences in grazing pressure between the vegetation types could be attributed to variation in shoot density.

Intake rates were related to the size of grass shoots (Fig. 5). The slopes of the regression lines for the three vegetation types were similar (the *F*-statistic associated with the interaction between vegetation type and shoot size was $F_{2,39} = 0.14$, $p > 0.05$), but the intercepts of the regression appeared to be different ($F_{2,41} = 10.27$, $p < 0.0005$). This means that the intake rate was not only dependent on the size of the grasses, but also on factors like growth form, or the amount of dead material covering the green shoots. After 10 May, when

Table 1
Vegetation types and percentage cover ± standard deviation for Laanan and Sandvaer. Mean values for May 1990–1992

Vegetation type	Grass	Dead	Herbs	Moss	Bare	n
Puccinellia-meadow	53.6 ± 20.7	10.0 ± 10.5	0.0 ± 0.0	0.0 ± 0.0	36.4 ± 18.0	11
Festuca-meadow	8.8 ± 6.8	48.8 ± 26.3	0.9 ± 2.7	2.0 ± 4.2	40.3 ± 25.0	108
Moss-heath	4.7 ± 2.0	13.0 ± 10.4	2.8 ± 5.2	52.3 ± 23.7	27.2 ± 32.4	45
Hay-meadow	53.0 ± 22.8	34.0 ± 24.6	0.0 ± 0.0	2.0 ± 4.5	8.0 ± 7.6	5
Herb-meadow	6.7 ± 7.5	50.8 ± 34.1	4.3 ± 9.8	6.0 ± 8.2	32.1 ± 35.6	90

Table 2
Occurrence of vegetation types (% area) on Laanan and on Sandvaer subdivided into Home and Outer islands (see text)

	Archipelago and year					
	Laanan 1981		Laanan 1991		Sandvaer 1990	
Vegetation type	Home	Outer	Home	Outer	Home	Outer
Puccinellia-meadow	1	< 1	< 1	< 1	< 1	< 1
Festuca-meadow	10	16	10	16	3	12
Moss-heath	12	45	5	12	9	24
Hay-meadow	43	< 1	3	< 1	42	10
Herb-meadow	4	4	36	24	30	7
other (buildings, shrubs, etc.)	30	35	46	48	16	47

Table 3
Cumulative number of goose droppings per m^2 ± standard deviation (with the number of samples in parentheses) in each of the vegetation types by island type and year

	Archipelago and year					
	Laanan 1981		Laanan 1991		Sandvaer 1990	
Vegetation type	Home	Outer	Home	Outer	Home	Outer
Puccinellia-meadow	12.3 ± 5.1 (10)	–	–	–	–	–
Festuca-meadow	13.4 ± 7.9 (17)	13.3 ± 6.3 (10)	11.9 ± 7.8 (33)	10.4 ± 5.7 (37)	13.5 ± 5.7 (4)	12.7 ± 4.5 (38)
Moss-heath	4.9 ± 3.8 (6)	8.1 ± 7.8 (20)	–	9.1 ± 5.2 (21)	7.1 ± 3.9 (3)	3.7 ± 4.4 (61)
Hay-meadow	14.6 ± 4.8 (11)	–	–	–	10.0 ± 6.3 (25)	–
Herb-meadow	6.5 ± 2.8 (6)	–	4.9 ± 4.3 (18)	2.7 ± 2.4 (16)	6.4 ± 4.5 (45)	7.0 ± 1.6 (5)

geese had heavily grazed most of the islands, intake rates had dropped to a similar value in the three vegetation types ($F_{2,12} = 0.05$, $p > 0.05$) at an average of 0.19 g min^{-1}.

5. Discussion

5.1. Are traditional areas used at carrying capacity?

The shift in distribution by barnacle geese staging in Norway from semi-natural islands to larger, agricultural islands may have been caused by two different mechanisms. Either, geese were driven from the traditional areas by a lack of resources, or geese had discovered a new and more profitable habitat which from then on has attracted increasing numbers. To distinguish between the two mechanisms, we have to explore whether the traditional islands were used up to carrying capacity, e.g. in the first case, exploitation of the traditional area should have remained maximal over years, whereas in the latter case, the area would be expected to become under-exploited. Goss-Custard (1985) defined carrying capacity as the density at which for every new bird that arrives in the area another bird must either emigrate or die. Our observations seem to meet this definition, as throughout the period of observation, the total population of barnacle geese showed a tremendous growth, whereas the density of birds on *Festuca*-meadows and hay-meadows (measured as total grazing pressure) remained constant over years. The use of moss-heath and herb-meadow was more variable, but this might have been caused by a larger variation in plant composition both within and between years. It is unlikely that the density of birds *per se* limited goose numbers. On the Home islands, densities were at most 74 birds ha^{-1} (a peak number of 400 birds on 5.4 ha of suitable habitat), whereas densities in flocks were well
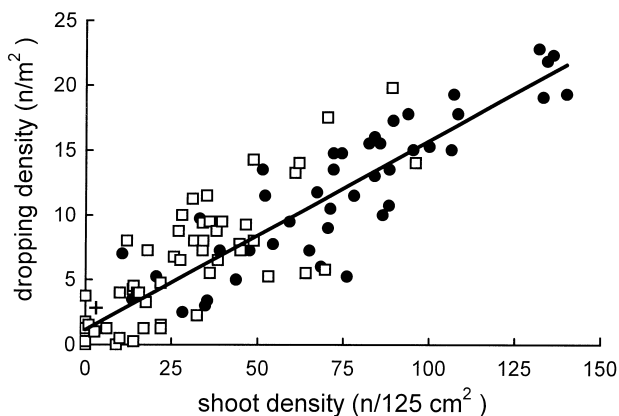
Fig. 4. Relationship between dropping density and shoot density for *Festuca*-meadows (●) and herb-meadows (□). For clarity, only the average value for moss-meadows (+) is given, but the regression line is for all three vegetation types combined ($y = 0.14x + 1.93$, $n = 167$, $r^2 = 0.72$, $p < 0.0005$).

beyond 600 birds ha^{-1} (Prop, unpublished). Instead, it is more likely that the number of birds was determined by the availability of food. In the first place, this became apparent from the positive relationship between grazing pressure and shoot density (Fig. 4). Moreover, as geese repeatedly visited the islands, plants were intensively grazed and food stocks declined through time. As a consequence, the intake rate dropped drastically (Fig. 5). The observations in different vegetation types suggested that geese did not accept an intake rate below $0.19 \, g \, min^{-1}$. This value is close to the intake rate of $0.15 \, g \, min^{-1}$ the geese should achieve to maintain constant body mass—assuming that geese require $1000 \, kJ \, day^{-1}$ (Drent et al., 1979), the feeding time is $907 \, min \, day^{-1}$ (Black et al., 1991), the metabolizable energy content of the food is $7.9 \, kJ \, g^{-1}$ on an ash-free basis (Prop and Vulink, 1992) and the ash content of the food is 5% (Prop, unpublished). By finely adjusting grazing to food availability, the geese, thus, ensure that

they obtain the body reserves required for migration. As a consequence of this mechanism, some individuals have to seek a new area when much of the food resources have been depleted. The incidence of birds that were observed by Black et al. (1991) on traditional islands, and that later in the season moved to agricultural areas, supports this idea.

5.2. Carrying capacity and management

Although the grazing pressure for the main vegetation types was similar over the years, the numbers in the traditional area declined because the vegetation changed towards types with a low density of grass shoots. The hay-meadows, which were one of the vegetation communities preferred by geese, had developed through long-sustained traditional management (Gullestad et al., 1984; Elven et al., 1988). But c. 12 years after cessation of cattle grazing and hay cutting, they had almost completely disappeared from the islands, and had been replaced by herb-meadows, which sustain much fewer geese. The disappearance of the hay-meadows has been aided by voles, which were formerly controlled with traps and dogs (A. Johnsen, personal communication). Apparently, the voles were so effective at removing below-ground vegetation during periods of snow cover in winter and spring that considerable areas became devoid of all vegetation. The importance of appropriate management is supported by the observation that numbers in still managed (and habited) archipelagoes within the traditional range remained constant over the years (Sandvaer), or even showed an increase (Hysvaer).

The role of human management in maintaining a short, grass-rich meadow has been widely documented (e.g. Cadwalladr et al., 1972; Wielgolaski, 1975; Bakker, 1978; Jones et al., 1982), and the importance of grassland management to obtain a sward suitable for geese is well recognized (Owen, 1973, 1975). Bakker et al. (1997) showed that a lowered stocking rate on a German salt-marsh caused a drop in goose usage in the following years by 30%. Similarly, the drastic decline in numbers of barnacle geese in the abandoned archipelagoes in Norway from 3000 (41% of the total population) in the early 1980s by approximately 67% to < 1000 (8% of the population) in the 1990s shows the converse effect of unfavourable management.

5.3. Range expansion

An increasing population and a decrease of the carrying capacity of the staging islands must have forced the geese to find new staging sites. We can identify two factors that have allowed the geese to expand their range during 1983–1992. First, the timing of migration and the routes taken by geese are in delicate balance
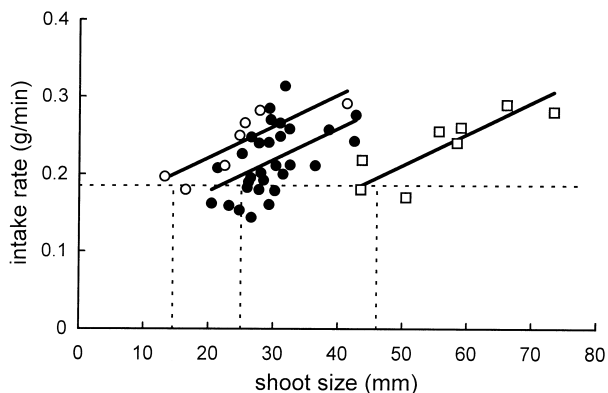

Fig. 5. Relationship between intake rate and shoot size for *Festuca*-meadows (●), hay-meadows (○) and herb-meadows (□). The dashed lines indicate the averages of intake rate (horizontal) and of shoot sizes (vertical) after 10 May.

with the spring growth of food (the green-wave-hypothesis; Drent et al., 1979). Thus, the geese presumably chose Helgeland as their traditional spring haunt on their way from the British wintering grounds to Spitsbergen because the spring flush largely coincided with their journey; whereas, the vegetation in more southerly locations had grown beyond their usefulness, vegetation in the north was still frozen (Deinum et al., 1981). We therefore assume that the observed change in weather conditions along the Norwegian coast towards warmer spring temperatures has made more northerly islands available to migrating barnacle geese. If global climate develops as current trends indicate (Schneider, 1989; Charlson and Wigley, 1994), we may even expect a further shift in the staging area of barnacle geese towards the north.

Secondly, a change in agricultural practice has made farmland more attractive to geese. During the past few decades, new varieties of plants, better drainage of fields, and applying more fertilizer have resulted in earlier, more nutritious crops in spring (Owen, 1980). These developments do not only take place in Norway, but occur on a global scale. Indeed, many goose populations have responded to these new resources (Madsen, 1985, 1987) in addition to traditionally used natural plant communities (Ebbinge et al., 1982). However, this has coincided with the destruction of the traditional habitat, or an increase of the population size (Madsen, 1987; Stroud et al., 1987; Gauthier et al., 1988; Leito, 1991; Ebbinge, 1992; Ganter, 1994) which makes it difficult to tell whether geese use agricultural crops by preference or because they have no other choice. However, in the case of the barnacle geese in Norway, birds still fully use the traditional habitat. So we infer that the agricultural fields function as a spill-over area.

5.4. Management implications

If emigration by island peoples from the Norwegian archipelagoes continues, and if the reduction in carrying capacity were to occur in all archipelagoes, we may cautiously predict the future distribution of geese over the staging area. Thus, of the 4000 geese still found on islands partly in human use, only 1320 geese would remain, while the majority would be deflected towards the larger agricultural islands closer to the mainland. This could have fitness consequences for the geese, as feeding exclusively on agricultural crops impairs the accumulation of body reserves (Prop and Black, unpublished). Moreover, larger numbers on the agricultural islands may cause increasing conflicts with local farmers. Currently, the geese use two agriculturally managed islands, including c. 10 farms (Bjøru, 1987; Black et al., 1991), but neighbouring islands and the mainland have similar habitats. As with other small farming communities, some farmers find the goose situation unacceptable (Paterson, 1991; Percival, 1993). Two lines of management could be followed to alleviate future conflicts. First, the carrying capacity of traditionally used islands could be enhanced by promoting the transformation of herb-meadows into hay-meadows. Some pilot experiments by a landowner of the Laanan archipelago, using sheep combined with burning and mowing of the vegetation, seemed to be effective in attracting more geese in the years 1985–1986 (Black et al., 1991). Secondly, an improvement in the quality of the saltmarshes on the larger islands may induce the geese to spend more time on the marshes instead of the fields. Some farms could be managed specifically for the geese in order to lessen conflict at the other farms (the refuge strategy; Owen, 1990).

References

Bakker, J.P., 1978. Changes in a salt-marsh vegetation as a result of grazing and mowing—a five-year study of permanent plots. Vegetatio 38, 77–87.

Bakker, J.P., Esselink, P., van der Wal, R., Dijkema, K.S., 1997. Options for restoration and management of coastal salt marshes in Europe. In: Urbanska, K.M., Webb, N.R., Edwards, P.J. (Eds.), Restoration Ecology and Sustainable Development. Cambridge University Press, Cambridge, pp. 286–322.

Bjøru, R., 1987. Forebyggende tiltak mot gaaseskader paa dyrka jord. En undersøkelse fra Herøy i Nordland, 1985 og 1986. Rapport 2-87, Fylkesmannen i Nordland.

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

Cadwalladr, D.A., Owen, M., Morley, J.V., Cook, R.S., 1972. Wigeon (*Anas penelope*) conservation and salting pasture management at Bridgwater Bay National Nature Reserve, Somerset. Journal of Applied Ecology 9, 417–425.

Charlson, R.J., Wigley, T.M.L., 1994. Sulfate aerosol and climate change. Scientific American 270, 28–35.

Davies, A., 1981. Tissue turnover in the sward. In: Hodgson, J., Baker, R.D., Davies, A., Laidlaw, A.S., Leaver, J.D. (Eds.), Sward Measurement Handbook. British Grassland Society, Hurley, UK, pp. 179–205.

Deinum, B., de Beyer, J., Nordtfeldt, P.H., Kornher, A., Ostgard, O., van Bogaert, G., 1981. Quality of herbage at different latitudes. Neth. J. Agr. Sci. 29, 141–150.

Drent, R.H., Ebbinge, B., Weijand, B., 1979. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. Verh. Ornith. Gesellsch. Bayern 23, 239–264.

Ebbinge, B.S., 1991. The impact of hunting on mortality rates and spatial distribution of geese wintering in the western palearctic. Ardea 79, 197–210.

Ebbinge, B.S., 1992. Regulation of numbers of Dark-bellied Brent Geese *Branta bernicla bernicla* on spring staging sites. Ardea 80, 203–228.

Ebbinge, B., StJoseph, A., Prokosh, P., Spaans, B., 1982. The importance of spring staging areas for Arctic-breeding geese, wintering in Western Europe. Aquila 89, 249–258.

Elven, R., Alm, T., Edvardsen, H., Fjelland, M., Fredriksen, K.E., Johansen, V., 1988. Botanical Protection Values on Seashores in Nordland, N Norway. A General Introduction. Locality Descriptions, S Helgeland Region. Økoforsk Rapp., 2A.

Ganter, B., 1994. Site tenacity and mobility of staging Barnacle Geese. Ardea 82, 231–240.

Gauthier, G., Bédard, Y., Bédard, J., 1988. Habitat use and activity budgets of Greater Snow Geese in spring. Journal of Wildlife Management 52, 191–201.

Goss-Custard, J.D., 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In: Sibly, R.M., Smith, R.H. (Eds.), Behavioural Ecology: Ecological Consequences of Adaptive Behaviour. Blackwell Scientific, Oxford, pp. 169–188.

Groot Bruinderink, G.W.T.A., 1989. The impact of wild geese visiting improved grasslands in the Netherlands. Journal of Applied Ecology 26, 131–146.

Gullestad, N., Owen, M., Nugent, M.J., 1984. Numbers and distribution of Barnacle Geese *Branta leucopsis* on Norwegian staging islands and the importance of the staging area to the Svalbard population. Norsk Polarinst. Skr. 181, 57–66.

Jones, M.B., Collett, B., Brown, S., 1982. Sward growth under cutting and continuous stocking managements: sward canopy structure, tiller density and leaf turnover. Grass and Forage Science 37, 67–73.

Keatinge, J.D.H., Stewart, R.H., Garrett, M.K., 1979. The influence of the temperature and soil water potential on the leaf extension rate of perennial ryegrass in Northern Ireland. J. Agric. Sci. 92, 175–183.

Leito, A., 1991. A note on migration ecology, population status and interactions with agriculture of Barnacle Geese *Branta leucopsis* in Estonia. Ardea 79, 347–348.

Madsen, J., 1985. Habitat selection of farmland feeding geese in West Jutland, Denmark: an example of a niche shift. Ornis Scand. 16, 140–144.

Madsen, J., 1987. Status and management of goose populations in Europe, with special reference to populations resting and breeding in Denmark. Danish Rev. Game Biol. 12, 1–76.

Madsen, J., 1991. Status and trends of goose populations in the western Palearctic in the 1980s. Ardea 79, 113–122.

Madsen, J., 1992. Waterfowl causing damage to agricultural crops in Europe: current status and habitat use. In: van Roomen, M., Madsen, J. (Eds.), Waterfowl and Agriculture: Review and Future Perspective of the Crop Damage Conflict in Europe. IWRB, Slimbridge, UK, pp. 21–32.

Owen, M., 1971. The selection of feeding site by White-fronted Geese in winter. Journal of Applied Ecology 8, 905–917.

Owen, M., 1973. The management of grassland areas for wintering geese. Wildfowl 24, 123–130.

Owen, M., 1975. Cutting and fertilizing grassland for winter goose management. Journal of Wildlife Management 39, 163–167.

Owen, M., 1980. The role of refuges in wildfowl management. In: Wright, E.N., Inglis, I.R., Feare, C.J. (Eds.), Bird Problems in Agriculture. British Crop Protection Council, London, pp. 144–156.

Owen, M., 1990. The damage–conservation interface illustrated by geese. Ibis 132, 238–252.

Owen, M., Black, J.M., 1991. Geese and their future fortune. Ibis 133 (Suppl. 1), 28–35.

Owen, M., Black, J.M., Agger, M.K., Campbell, C.R.G., 1987. The use of the Solway Firth, Britain, by Barnacle Geese *Branta leucopsis* Bechst. in relation to refuge establishment and increases in numbers. Biological Conservation 39, 63–81.

Owen, M., Norderhaug, M., 1977. Population dynamics of Barnacle Geese (*Branta leucopsis*) breeding in Svalbard, 1948–1970. Ornis Scand. 8, 161–174.

Pannekoek, J., van Strien, A.J., 1994. Developments in wildlife statistics: new methods for meeting new demands. Netherlands Official Statistics 9, 42–45.

Paterson, I.W., 1991. The status and breeding distribution of Greylag Geese *Anser anser* in the Uists (Scotland) and their impact upon crofting agriculture. Ardea 79, 243–252.

Peacock, J.M., 1975. Temperature and leaf growth in *Lolium perenne*. Journal of Applied Ecology 12, 99–114.

Percival, S.M., 1993. The effects of reseeding, fertilizer application and disturbance on the use of grasslands by Barnacle Geese, and the implications for refuge management. Journal of Applied Ecology 30, 437–443.

Prop, J., Deerenberg, C., 1991. Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. Oecologia (Berlin) 87, 19–28.

Prop, J., Loonen, M., 1989. Goose flocks and food exploitation: the importance of being first. Proc. Int. Ornithol. Congr. 1986, Ottawa, pp. 1878–1887.

Prop, J., Vulink, T., 1992. Digestion by Barnacle Geese in the annual cycle: the interplay between retention time and food quality. Funct. Ecol. 6, 180–189.

Schneider, S.H., 1989. The changing climate. Scientific American 261, 28–36.

Stroud, D.A., Reed, T.M., Pienkowski, M.W., Lindsay, R.A., 1987. Birds, Bogs and Forestry. The Peatlands of Caithness and Sutherland. NCC, Peterborough, UK.

Underhill, L.G., Prys-Jones, R.P., 1994. Index numbers for waterbird populations. I. Review and methodology. Journal of Applied Ecology 31, 463–480.

Westhoff, V., Van der Maarel, E., 1978. The Braun–Blanquet approach. In: Whittaker, R.H. (Ed.), Classification of Plant Communities. Junk, The Hague, pp. 287–399.

Whittaker, R.H., 1967. Gradient analysis of vegetation. Biol. Rev. 42, 207–264.

Wielgolaski, F.E., 1975. Comparison of plant structure on grazed and ungrazed tundra meadows. In: Wielgolaski, F.E. (Ed.), Fennoscandian Tundra Ecosystems. Part 1. Plants and Microorganisms. Springer, New York, pp. 86–93.