

FORAGING BEHAVIOUR AND SITE SELECTION OF BARNACLE GEESE *Branta leucopsis* IN A TRADITIONAL AND NEWLY COLONISED SPRING STAGING HABITAT

JEFFREY M. BLACK¹, CHARLOTTE DEERENBERG² & MYRFYN OWEN¹

ABSTRACT For three weeks in May the Svalbard Barnacle Geese *Branta leucopsis* stop to feed on the archipelagos of the Helgeland district, up to 50 km out to sea off western Norway. However, since 1980 an increasing part of the population has moved to a newly exploited agricultural habitat closer to the mainland. This paper compares the foraging performance of geese using the traditional and the new area. Differences between the habitats include asymmetries in time budgets, plant quality, feeding performance and abdominal fatness. We speculate on the relative merits of remaining in previously experienced habitats or moving to unexplored areas. There is some indication that younger geese are less loyal to old sites and are moving to the agricultural habitat. In 1988 18.3% of the geese using the agricultural fields successfully brought offspring back to Scotland compared to 9.6% for the outer island birds, although this difference was not statistically significant.

¹The Wildfowl Trust, Slimbridge, Gloucester, GL2 7BX, UK. ²Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

INTRODUCTION

Within a stable population and a fixed environment individuals tend to show little variability in behaviours. However, when selection pressures change or become unpredictable individuals are prone to more exploratory strategies (Maynard Smith 1982, Parker 1984). Those that successfully exploit a new or altering environment could have a significant effect on the productivity of the population as a whole (Parker 1985).

The Svalbard/Solway population of Barnacle Geese *Branta leucopsis*, which is considered in this paper, is currently exposed to two potentially destabilizing effects: changes in the quality of their traditional spring staging habitat and a dramatic increase in population. Spring observations in Norway showed that since 1980 an increasing number of the geese had ranged away from the maritime outer island habitat to feed on small agricultural fields on larger islands nearer the mainland (see Gullestad *et al.* 1984). Spring fattening and nutrient

accumulation are critical in determining the reproductive potential in arctic breeding geese (Ryder 1970, Ankney & McInnes 1978, Ebbinge *et al.* 1982) and the geese using these two habitat types could differ in productivity. By assessing the patterns of usage, food quality, foraging behaviour and body condition we examine the profitability of the two habitats. We test the hypothesis that the agricultural fields are a good alternative to the original habitat by comparing food quality and by checking the actual reproductive success of individuals which used the two different habitats in 1986-1988.

BACKGROUND AND METHODS

Svalbard Barnacle Geese undergo two periods of spring fattening: the first is on the Solway Firth, Scotland, before a 1500 km migration to Helgeland, Norway (65-66° N, 11° E), and in Norway prior to another 1500 km flight to the Spitsbergen breeding grounds (77-80° N, 15° E). The fat re-

erves (as determined by an abdominal profile index) expended during the first migration are at least partially replenished in Norway (Owen 1981, Black & Owen 1988). The Helgeland area consists of about 20 archipelagos, over 2000 islands in total. Those closer to the mainland are fairly large, 10-20 m high and covered with heather *Calluna vulgaris*. The majority of the geese feed on smaller islands that are flat and less than 5m high and covered with a salt tolerant sward of mainly *Festuca rubra* and some *Puccinellia maritima*.

Since 1975 our primary study sites have been on the outer islands, particularly the Laanan/Flovær complex which is 35 km from the mainland (Gullestad *et al.* 1984): this paper includes observations from 1986 and 1987. The Laanan home island (10 ha), where up to 20 houses or barns stand, is in the centre of 300 small islands. The last permanent habitation was in 1979 and until then a small number of sheep was kept, hay was cut and some areas were burned. Left unmanaged the vegetation grows up to 1 m high and the layer of dead grass makes early spring growth less obtainable to the geese. The study area in 1988 was on two relatively large islands, South-Herøy and Tenna, 15 km from the mainland. The community of 1000 people includes 10 small agricultural holdings: most fields are less than 0.5 ha and the total arable area is about 100 ha. In spring and summer sheep and cattle graze the coasts and some fertilized grasslands in late summer. The fields are reseeded with mixtures of predominantly *Phleum* sp. which is harvested green or cut for hay. Tall vegetation on coasts is burned in late summer or early April. In 1988 we also visited another archipelago, Sandvær, 30 km out to sea, which is still inhabited and the vegetation is managed in the traditional way as was Laanan in previous decades.

Flock behaviour was assessed by identifying the number of geese feeding, resting, preening, vigilant and socially involved. Peck and step rates were registered in different habitats by recording the time for 100 pecks (backward head movements) and for 20 steps. About 20% of the population had individual rings (Owen 1984); the data collected on ringed individuals included the mate's

identity, number of offspring, abdominal profile index and location.

Grazing intensity was assessed by dropping counts (Owen 1971). Droppings were collected at 5 day intervals from 15-20 plots (4 m²) in 7 agricultural fields. To identify the diet, fresh droppings were collected from sites where the geese had been feeding for at least one hour: retention time is about one hour (Owen 1975, Ebbinge *et al.* 1975). Samples of droppings were dried, weighed and later analysed microscopically for species composition (Owen 1975). We estimated faecal output (g dry per hour) by correcting mean weights per dropping for mean interval time.

Species composition of the fields was estimated using a point-quadrat method: 10 evenly distributed quadrats were sampled and per quadrat 20 individual plants were identified at intervals of 10 cm. Individual shoots of the grasses *Phleum pratense*, *Poa* sp., *Festuca rubra* and *Anthoxanthum odoratum* were marked in small plots which were evenly distributed over the selected site. The plots were paired, of which one had grazing animals excluded. Every 5 days the exclosures were exchanged after measuring blade lengths to the nearest mm (see Prop *et al.* 1984) of all marked shoots. Growth was defined as the increment of all blades of a shoot and expressed as mm/shoot. Samples of *Phleum*, *Poa* and *Festuca* were plucked by hand, sorted into green and dead material, weighed, dried, reweighed and stored. Grass samples were later analysed for total nitrogen content by a modified Kjeldahl method that includes nitrate (Mr. Deys, University Nijmegen). Crude protein values were calculated by multiplying N-content by 6.25; the values are expressed as percentage of dry weight.

RESULTS

Attendance pattern and distribution

Figure 1 shows two years' data on the timing of the departure of the geese from Scotland and their arrival in Norway. The non-stop journey is thought to take 24 hours in still air (Gullestad *et*

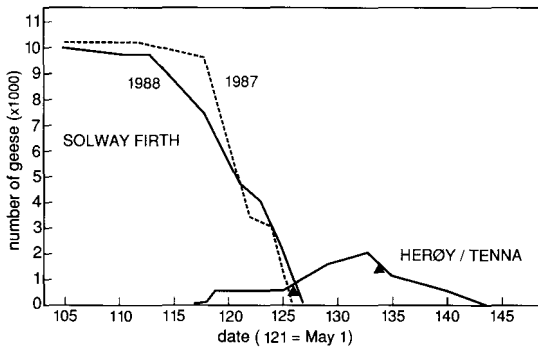


Fig. 1. Timing of spring migration from the Solway Firth, Scotland, to the agricultural habitat (Herøy/Tenna) in Helgeland, Norway. Dotted line (Scotland) and triangles (Norway) indicate data obtained in 1987.

al. 1984). Flocks were seen on Herøy/Tenna for a total of 27 days in 1988. Based on birds that were identified more than once, the mean length of stay was 8 ± 5 days ($n = 138$). Two birds were present for at least 20 days.

Gullestad *et al.* (1984) argue that the geese began to disperse from Laanan in the early 1980s because the vegetation on the home island was no longer managed. In 1983 7 sheep were returned to the home island and a neighbouring skerry. The number of sheep increased to 11 in 1984 but, because of conflicts with other interests, they were removed in 1987. In 1986 several areas of overgrown vegetation were burned one month before the geese arrived. These management techniques, together with the natural fertilizer from the sheep, appeared to attract the geese back to the home island (Fig. 2). The geese continued to use the area for one year after the end of the management regimes, e.g. 1980 and 1987.

From 1980 onwards an increasing number of birds has been invading the agricultural fields on Herøy/Tenna. Numbers rose from 50 in 1980 (1% of the population) to 500 in 1983 (6%), 1000 in 1986 (10%) (R. Bjørn pers. comm.), 1600 in 1987 (14%) and 1800 in 1988 (16%). This means that in 1988 the remaining 9000 geese were probably still utilizing outer island habitats which may vary in quality according to the extent of management that still exists. In 1988 emerging plants on Laanan were hindered by dead material and much of the topsoil was torn up by Water Voles *Arvicola terrestris*

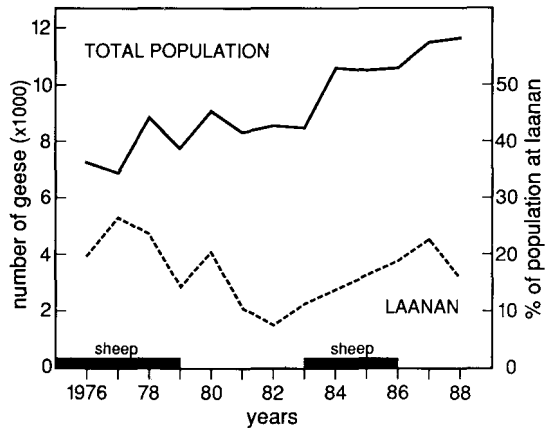


Fig. 2. The percentage of geese that used the Laanan archipelago between 1976 and 1988 in relation to management of the vegetation. The darkened area at the bottom axis denotes the presence of sheep (A. Johnsen, pers. comm.). Figures on total population are after Owen (1984) and Owen & Black (1990).

which had invaded the island. Only 100 birds were counted on the Laanan home island while in previous years flocks of over 1000 birds were regular.

In order to test if Laanan birds moved away from the unmanaged outer island habitat to the agricultural fields, we checked the records of birds that were seen in both 1987 and 1988. The majority of geese were seen in the same area in both years (90% of 146 birds); 12 of the 14 between year changes were away from Laanan to Herøy/Tenna ($\chi^2 = 28.7$, $df = 1$, $p < 0.01$). Within a year only 4 birds out of 800 individuals were seen in both places: first at Laanan and after 1-10 days at Herøy/Tenna.

Use of the agricultural area - Herøy/Tenna

Figure 3 depicts the pattern of visits by the geese to the agricultural fields and of returns to coastal roosts. The birds flew to the fields at sunrise and again in the afternoon between 15 00 and 18 00 h. Flocks took flight on average once every 40 min (8 h continuous watch) but usually they landed within minutes in the same or a neighbouring field. If there was a severe disturbance they flew to the adjacent coast for up to one hour. Fields were not visited in the middle of the day when human activi-

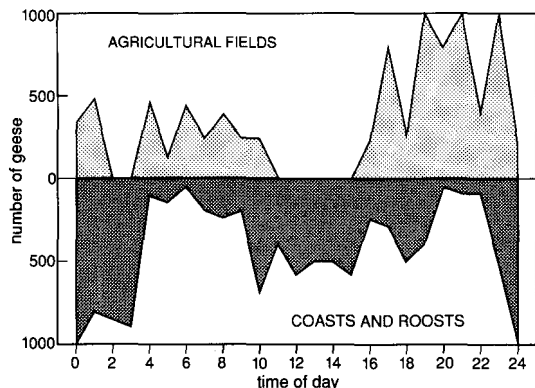


Fig. 3. The diurnal pattern of visitation to Herøy/Tenna agricultural fields (top) and to coastal areas (bottom) based on peak numbers observed during the study period.

ty was greatest nor at night unless the moon was evident. The predominant activity was recorded in the different areas; all the flocks on agricultural fields were feeding (100%, $n = 35$) whereas coasts were used primarily for resting (or as a retreat) (68%, $n = 47$) and for feeding (32%).

In order to establish the birds' fidelity to particular fields and coasts we kept track of flocks moving between sites. Very little interchange occurred

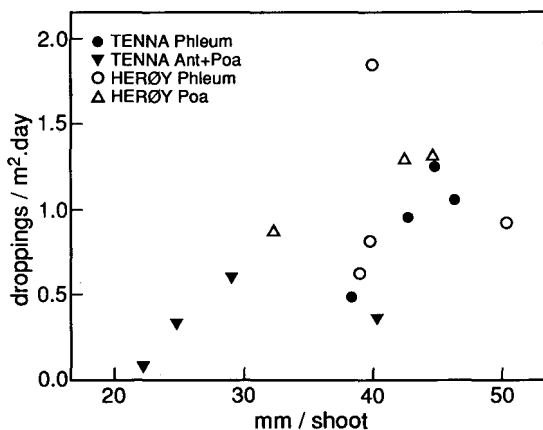


Fig. 4. Visitation to agricultural fields in relation to a green biomass index. The biomass index is here expressed as the cumulative length of the living blades per shoot by measuring individually marked plants prior to goose visits. The relationship was positive and significant ($r^2 = 0.44$, $n = 16$, $p < 0.01$).

between the two island study sites even though distances between the islands were similar to distances within island areas: 88% of the flocks that we monitored ($n = 65$) remained on the same island complex.

Visitation rates (as derived by number of droppings per m^2 per day) to individual fields were positively related to available biomass as determined by detailed measurements of individual grass plants (Fig. 4) and less so to the growth rate of those grass species (linear regression $r^2 = 0.21$, $n = 16$, $p < 0.06$). The amount of vegetation removed increased with the visitation rate (linear regression $r^2 = 0.21$, $n = 16$, $p < 0.01$).

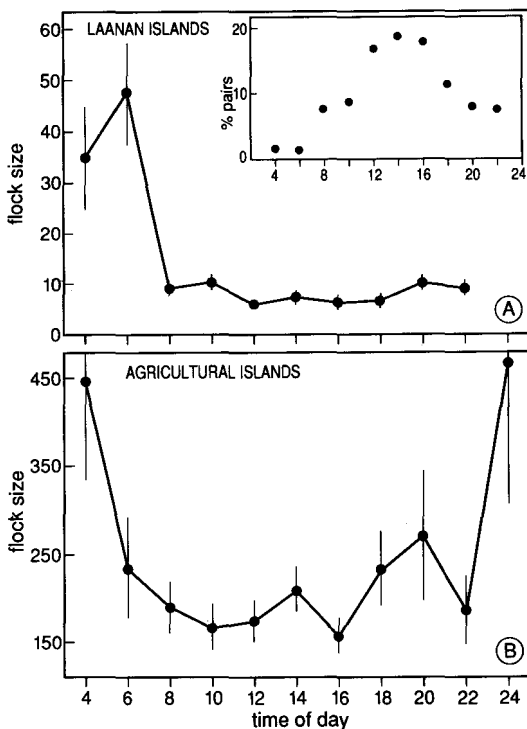


Fig. 5. Mean flock sizes throughout the day in the outer island area Laanan in 1986 (A) and the agricultural area Herøy/Tenna in 1988 (B). The stippled line in the upper figure shows that the proportion of flocks of two (= pairs) increases as soon as flocks depart from the home island and peaks in the afternoon. Sample sizes for outer island and agricultural points range from 22-112 counts to 4-27 respectively.

Comparison between agricultural sites and outer islands

Flocking behaviour and activity On Herøy/Tenna the geese visited areas of fertilized vegetation for up to 12 hours each day (see Fig. 3) which was considerably longer than outer island birds spent on naturally fertilized home island vegetation: a maximum of 6 hours per day (Gullestad *et al.* 1984, unpublished data from 1986-87). These patterns appear to affect both flock size and activity budgets in the two habitats.

In both habitats flock sizes were greatest in the early morning and in the evening (Fig. 5) but they were significantly larger on the agricultural habitat (hourly means, $t = 6.6$, $df = 19$, $p < 0.001$). In contrast to the situation on the agricultural area, pairs split from larger flocks to forage on their own in the middle of the day on the outer islands (Fig. 5 insert). Due to the tradeoff between vigilance and feeding, birds in pairs spent significantly less time feeding than those in small flocks (Table 1). Pairs in flocks did lose some feeding time because of conflicts with neighbours, but continuous watches on 24 pairs (140 min) revealed that this loss was negligible: only 10.5 s per hour in flocks of 4-10

Table 1. Female and male feeding time at Laanan with and without neighbours. The mean number of birds in flocks was 30 ± 30 (range 4-100). Data include paired birds only. See Fox & Madsen (1981) for a similar comparison in Greenland White-fronted Geese *Anser albifrons flavirostris*.

	In pairs		In flocks
Females	82.6%	**	90.7%
	(3.2)		(2.0)
	$n = 19$		$n = 21$
	***		***
Males	63.1%	**	76.5%
	(4.3)		(3.7)
	$n = 20$		$n = 22$

Standard error in parentheses, asterisks indicate results from Mann-Whitney U -tests between categories: **: $p < 0.02$; ***: $p < 0.01$.

birds and 13.4 s per hour in flocks of 12-30 birds.

Results from 255 flock scans showed that the birds' diurnal time budget in the two areas varied considerably for time spent feeding and resting (Fig. 6). Due to a continuous high level of feeding (overall mean 84%), outer island birds had less time for resting (4%) compared to geese using agricultural areas (70% feeding, 17% resting); other

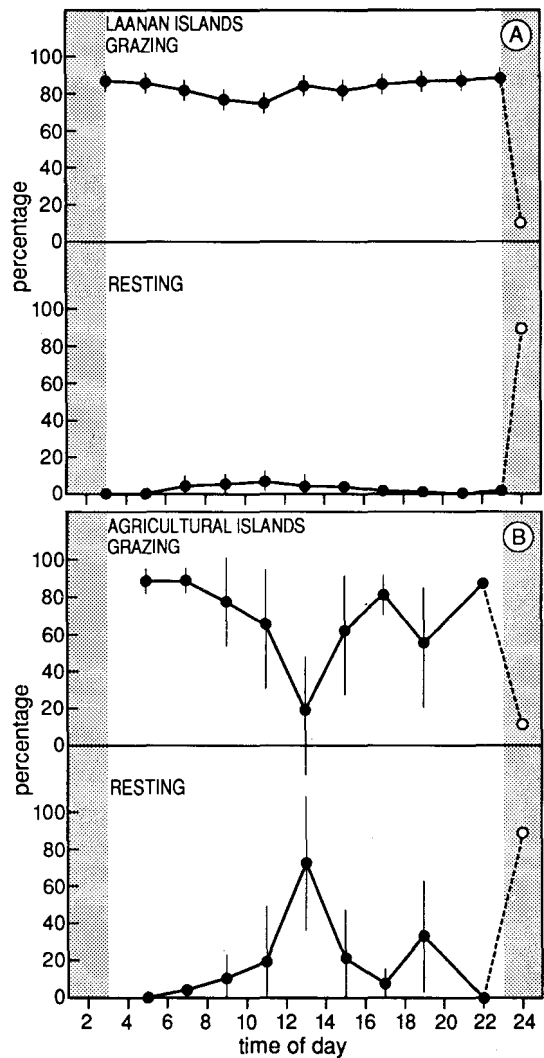


Fig. 6. The proportion of time the geese spent feeding and resting in outer islands (A) (mean number in scans = 131, $n = 99$) and agricultural areas (B) (mean = 124, $n = 156$) during the day.

activities were similar. The peck rate was significantly lower (111 pecks per min) and more variable (coefficient of variation, $cv = 41\%$) for geese feeding on the vegetation of coasts and outer islands than those feeding on agricultural fields (154 pecks per min, $cv = 28\%$) (difference in means, $t = 2.27$, $df = 40$, $p < 0.05$). There was no significant difference in step rates while feeding on natural or agricultural swards, but the trend was towards a faster rate on agricultural fields.

Diet Figure 7 depicts the relative diet of agricultural and outer island geese over the study period. In the first period, 27-30 April, the majority of the diet from agricultural islands was dead material, originating from coastal sites. The first few days after the geese arrived snow was still melting from the fields and grass growth had not yet begun. Thereafter, *Phleum* predominated in the diet but declined as the proportion of *Poa* increased. On the outer island (Sandvær), *Poa* was the prevailing species in the diet in the first and middle periods and *Festuca* at the last period. In both situations the geese selected different species from the same sward in different periods.

It appeared that *Phleum* was actively selected for as its occurrence in the vegetation of the agricultural fields was 33.4% of live biomass, whereas it reached 48% of the diet. The proportion of *Poa* in the vegetation was 47.7%, slightly above the level in the diet (data on the vegetation collected 17-18

Table 2. Protein content of the main foodplants on agricultural fields (Tenna) and on outer islands (Sandvær). Values obtained by analysis for total nitrogen.

date	Tenna		Sandvær	
	<i>Phleum</i>	<i>Poa</i>	<i>Festuca</i>	<i>Poa</i>
3 May			16.04%	17.93%
11 May	28.12%	24.42%		
19 May	37.85%*	32.09%*		
23 May			21.37%	

* from fields that were partially fertilized

May). Factors affecting selection may be nutrients (Owen *et al.* 1977, McNaughton 1979, reviewed in Prins & Ydenberg 1985) and available biomass by acting upon digestive efficiency and intake rate respectively (Owen 1981, Prop & Deerenberg in press). *Phleum* consistently contained more protein than either *Poa* or *Festuca* (Table 2) and also provided more biomass per shoot than *Poa* (ANOVA on cumulative length $F_{1,776} = 26.18$, $p < 0.01$, followed by *T*-tests) probably due to higher growth rates (Fig. 8). Growth rates of *Phleum* and *Poa* were significantly different in the last two periods (ANOVA $F_{1,776} = 53.64$, $p < 0.01$, *T*-tests). Data from outer island Sandvær are limited and give a lower protein value for *Festuca* than for *Poa* in early May (see Table 2).

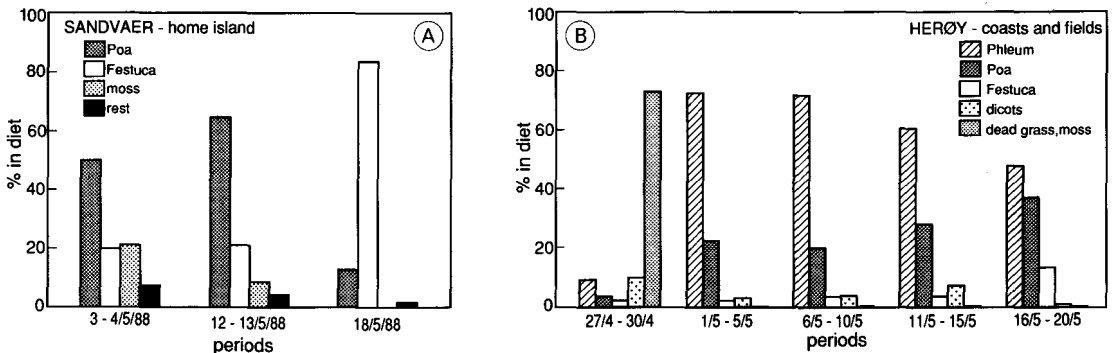


Fig. 7. The seasonal trend in diet for geese using an outer island (A) or an agricultural habitat (B). The data are based on 2-7 pooled samples of 10 droppings each. See text on comparison with available vegetation.

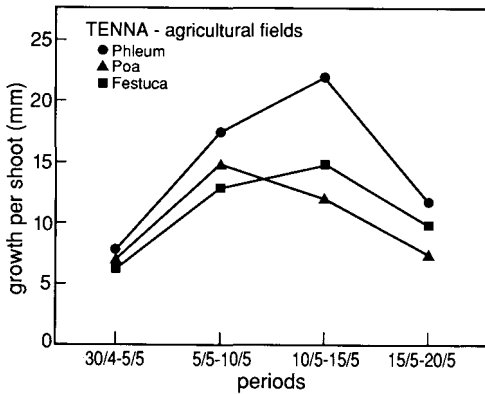


Fig. 8. Growth rates of three grass species throughout the spring staging period. Measurements were taken on 44-93 individual shoots of each species.

Body condition and reproductive success Figure 9 shows the increase of abdominal profiles of the birds from Herøy/Tenna. On four occasions data were collected from outer islands for comparison. The three measurements for Sandvær were closely similar to those from the agricultural habitat, but the single point from Laanan was significantly different ($\chi^2 = 62.2$, $df = 6$, $p < 0.001$). On 9 May the birds from Laanan had achieved profiles that the Herøy/Tenna birds had attained 3 days earlier.

Our final comparison was of the reproductive performance of birds using different habitats. In our experience, the majority of parents and offspring are still in family groups until the end of January (Black & Owen 1989a). By this time in 1989 just over 6600 records of individually marked birds were obtained at the wintering grounds in Scotland. We selected birds that were seen in one of the two areas in 1988 and that were known not to have

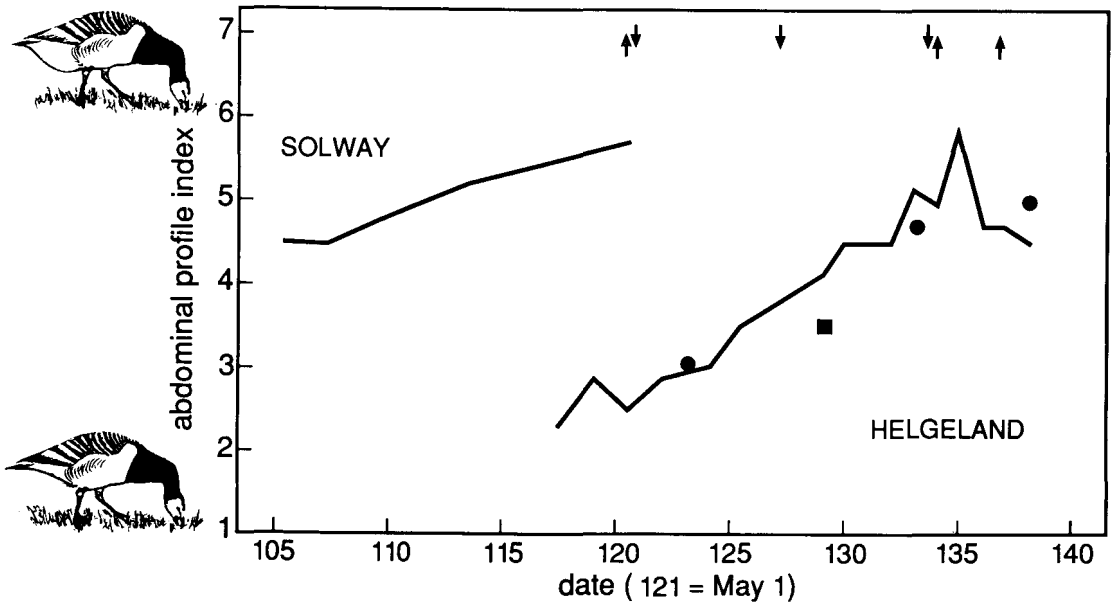


Fig. 9. The development of abdominal fatness throughout the study period of geese feeding on Herøy/ Tenna agricultural fields (solid line), Sandvær (spots) and Laanan (black square) outer islands. The index is a visual estimate of abdominal profile (see vignettes on ordinate); the values plotted are the weighted medians (median profile adjusted for numbers as follows $WM = MP \cdot (NM + NA - NB) / NM$, where MP : median profile, NM : number at median profile, NA : number above and NB : number below median profile). The arrows at the top show the timing of arrivals and departures from the area. After a departure abdominal profiles are much thinner indicating that the fattest birds departed.

Table 3. Observed reproductive success of geese using different spring staging areas in 1988 as determined by association with goslings on the wintering grounds.

Area	With goslings	Total	%
Laanan			
- outer islands	6	64	9.4
Sandvær			
- outer islands	2	19	10.5
Herøy/Tenna			
- agricultural fields	19	104	18.3

$\chi^2 = 2.8$, $df = 2$, $p < 0.30$, two-tailed test

switched between sites between years. We also included "traditional" Laanan birds: those known to have recently used the area i.e. seen in 1986 and/or 1987 and at least one previous year. Geese which were three years old or younger were excluded. The results are shown in Table 3. Although the results for this season suggest that geese utilizing the agricultural habitat in spring achieved a higher breeding success the difference was not significant.

DISCUSSION

Site loyalty is considered to be adaptive because of a residential effect on dominance and mate retention or attraction, and/or because incremented experience and knowledge about local resources and potential dangers enhance survival and breeding potential (Hinde 1956, Lack 1966, Gauthreaux 1978). We have shown that Barnacle Geese are extremely loyal to their spring staging areas between years and within the staging areas themselves (see also Gullestad *et al.* 1984). Obviously, however, some geese are less loyal since an increasing number has colonised an agricultural habitat in recent years. Many goose populations, world-wide, have colonised agricultural land in the last 20-30 years (see references in Owen 1980). In each case the change started with small flocks which increased in subsequent years. There are at least 3 possible

reasons documented why individuals change previously established routines:

(1) better resources elsewhere (Madsen 1985, Prins & Ydenberg 1985)

(2) depletion of original resources (Owen 1971, Charman 1979)

(3) competition avoidance (Zwarts 1975, Goss-Custard *et al.* 1984, Suntherland & Parker 1985).

In this study 9 out of the 12 individually marked geese that moved away from the outer islands to the agricultural area were less than three years old and unpaired. This implies that they moved because they were excluded by dominant, "traditional" outer island geese as formulated under (3), maybe because young unpaired geese are at the bottom of the social hierarchy (Black & Owen 1989b).

However, the first 2 possibilities are more directly addressed in this study. Although more extensive measurements are needed we provide some data showing that protein values of the main food-plants are lower at outer island sites than at agricultural fields. Protein contents of grasses sampled at Laanan in 1981 were in the same range as those from the outer islands in 1988 (*Poa* 20-25.6%, *Festuca* 20-22.7% and *Puccinellia* 29.3-32%, Nugent & Prop own obs.). Available biomass at the outer islands has not yet been assessed and may be crucial in determining carrying capacity and food intake. In addition the asymmetry in diet from the two habitats may be directly linked to the amount of fat and type of nutrient acquisition.

The foraging routines of the birds at the outer islands are characterised by a longer feeding day (16.8 h) and have a lower feeding rate (111 pecks per min) compared to geese exploiting the agricultural fields (14 h, 154 pecks per min). These differences fit the interpretation that feeding conditions are currently more favourable on the agricultural habitat. The interplay between lower **quality** of food on offer on the outer islands and the higher **quantity** of food that must be ingested to compensate for this remains to be quantified. We can easily imagine that geese are sampling the asymmetries in foraging profitability and that they are deciding to range further to find a more rewarding situation. Two lines of evidence suggest that the geese change

areas in the following rather than in the same season: the lag in declining numbers after management ceased in Laanan (Fig. 2) and the number and timing of resightings in new areas (4 within year and 14 between year changes).

Asymmetries in spring resource accumulation in habitats of different quality have been demonstrated for Greater Snow Geese *Anser caerulescens atlanticus* (Gauthier *et al.* 1984, Bédard & Gauthier 1989) and for Pink-footed Geese *Anser brachyrhynchus* (Madsen 1985). We provide some evidence that geese using an agricultural habitat in Norway were at one point three days in advance of those from outer islands in terms of their fatness. If this could be shown to be consistent and resulting in a larger amount of body reserves at the start of the second migration and at arrival at the breeding grounds on Spitsbergen a direct link to reproductive success may be achieved.

ACKNOWLEDGEMENTS

We are grateful to R. Bjørn, B. Kveum, J. Portlock, A.-H. Rønning and P. Shimmings for their steadfast collaboration and to A. Johnsen for his hospitality and support on Laanan. We also thank the landowners for access to their fields and the Herøy Kommune. The project was financed by The Wildfowl Trust and the Directorate for Nature Management of Nordland, Norway. C.D. in addition acknowledges assistance from the Groningen Universiteitsfonds and the Fonds Dr. Catherine van Tussenbroek Trust. We appreciate R. Drent's and M. Moser's comments on the paper.

REFERENCES

- Ankney, C.D. & C.D. McInnes 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459-471.
- Bédard, J. & G. Gauthier 1989. Comparative energy budgets of Greater Snow Geese *Chen caerulescens atlantica* staging in two habitats in spring. *Ardea* 77:3-20.
- Black, J.M. & M. Owen 1988. Variation in pair bond and agonistic behaviours in Barnacle Geese on the wintering grounds. In: M. Weller (ed.). *Wildfowl in winter* (pp. 39-57). University of Minnesota Press, Minneapolis.
- Black, J.M. & M. Owen 1989a. Parent-offspring relationships in wintering Barnacle Geese. *Anim. Behav.* 37:187-198.
- Black, J.M. & M. Owen 1989b. Agonistic behaviour in Barnacle Goose flocks: assessment, investment and reproductive success. *Anim. Behav.* 37:199-209.
- Charman, K. 1979. The feeding ecology and energetics of the Dark Bellied Brent Goose (*Branta bernicla bernicla*) in Essex and Kent. In: R.L. Jefferies & A.J. Davy (eds.). *Ecological processes in coastal environments* (pp. 451-465). Blackwell Scientific Publications, Oxford.
- Ebbinge, B., K. Canters & R. Drent 1975. Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. *Wildfowl* 26:5-19.
- Ebbinge, B., A. St. Joseph, P. Prokosh & B. Spaans 1982. The importance of spring staging areas for arctic breeding geese, wintering in western Europe. *Aquila* 89:249-258.
- Fox, A.D. & J. Madsen 1981. The pre-nesting behaviour of the Greenland White-fronted Goose. *Wildfowl* 32:48-54.
- Gauthier, G., J. Bédard, J. Huot & Y. Bédard 1984. Spring accumulation of fat by Snow Geese in two staging habitats. *Condor* 86:192-199.
- Gauthreaux, S.A. 1978. The ecological significance of behavioural dominance. In: P.P.G. Bateson & P.H. Klopfer (eds.). *Perspectives in ethology* (pp. 17-54). Plenum, New York.
- Goss-Custard, J.D., R.T. Clarke & S.E.A. Durell 1984. Rates of food intake and aggression of Oystercatchers *Haematopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe estuary. *J. Anim. Ecol.* 53:233-246.
- Gullestad, N., M. Owen & M. Nugent 1984. Numbers and distribution of Barnacle Geese *Branta leucopsis* on Norwegian staging islands and the importance of the staging area to the Svalbard population. *Nor. Polarinst. Skr.* 181:57-65.
- Hinde, R.A. 1956. The biological significance of the territories of birds. *Ibis* 98:340-369.
- Lack, D. 1966. *Population studies of birds*. Oxford University Press, Oxford.
- Madsen, J. 1985. Relations between spring habitat selection and daily energetics of Pink-footed Geese *Anser brachyrhynchus*. *Ornis Scand.* 16:222-228.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am. Nat.* 113:691-703.

- Owen, M. 1971. The selection of feeding sites by White-fronted Geese in winter. *J. Appl. Ecol.* 8:905-917.
- Owen, M. 1975. An assessment of faecal analysis technique in waterfowl feeding studies. *J. Wildl. Manage.* 39:271-279.
- Owen, M. 1980. *Wild geese of the world*. Batsford, London.
- Owen, M. 1981a. Abdominal profile - a condition index for wild geese in the field. *J. Wildl. Manage.* 29: 227-230.
- Owen, M. 1984. Dynamics and age structure of an increasing goose population - the Svalbard Barnacle Goose. *Nor. Polarinst. Skr.* 181:37-47.
- Owen, M. & J.M. Black 1990. Barnacle Geese. In: I. Newton (ed.). *Lifetime reproductive success in birds*. Academic Press, Oxford.
- Owen, M., M. Nugent & N. Davies 1977. Discrimination between grass and nitrogen fertilized vegetation by young Barnacle Geese. *Wildfowl* 28.
- Parker, G.A. 1984. Evolutionary stable strategies. In: J.R. Krebs & N.B. Davies (eds.). *Behavioural ecology: an evolutionary approach*. Blackwell Scientific Publications, Oxford.
- Parker, G.A. 1985. Population consequences of evolutionarily stable strategies. In: R.M. Sibly & R.H. Smith (eds.). *Behavioural ecology: Ecological consequences of adaptive behaviour* (pp. 33-58). Blackwell Scientific Publications, Oxford.
- Prins, H.H.Th. & R.C. Ydenberg 1985. Vegetation growth and a seasonal habitat shift of the Barnacle Goose (*Branta leucopsis*). *Oecologia* (Berlin) 66: 122-125.
- Prop, J. & C. Deerenberg in press. Feeding constraints in spring staging Brent Geese and the impact of diet on the accumulation of body reserves. *Oecologia* (Berlin).
- Prop, J., M.R. van Eerden & R.H. Drent 1984. Reproductive success of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. *Nor. Polarinst. Skr.* 181:87-117.
- Ryder, J.P. 1970. A possible factor in the evolution of clutch size in Ross' Goose. *Wilson Bull.* 82: 1083-1102.
- Suntherland, W.J. & G.A. Parker 1985. Distribution of unequal competitors. In: R.M. Sibly & R.H. Smith (eds.). *Behavioural ecology: Ecological consequences of adaptive behaviour* (pp. 255-274). Blackwell Scientific Publications, Oxford.
- Zwarts, L. 1975. Density-related processes in feeding dispersion and feeding activity of Teal (*Anas crecca*). *Ardea* 64:192-209.

SAMENVATTING

De Brandganzen die op Spitsbergen broeden en in Schotland overwinteren pleisteren in mei gedurende ongeveer drie weken op Noorse eilanden die tot op 50 km uit de kust liggen, iets ten zuiden van de poolcirkel. Het aantal pleisterende ganzen hangt samen met het agrarisch beheer van het eiland. Het aantal ganzen is groter wanneer er schapen worden gehouden dan wanneer het eiland aan zijn lot wordt overgelaten (Fig. 2).

Sedert 1980 verplaatst een toenemend deel van de populatie zich naar eilanden met gecultiveerde graslanden die dichter bij het vasteland liggen. Daarbij zijn relatief veel jonge ongepaarde ganzen betrokken. In dit artikel wordt nagegaan in hoeverre deze verplaatsing kan worden verklaard door een verbetering van de voedselomstandigheden.

De gecultiveerde graslanden, waarin *Phleum pratense* (timotheegras) domineert, worden 's ochtends vroeg en laat in de namiddag bezocht door de ganzen (Fig. 3). De bezoekenintensiteit, gemeten aan keuteldichtheden, is positief gecorreleerd met de aanwezige biomassa (Fig. 4). Op de eilanden met gecultiveerde graslanden verblijven de ganzen meestal in grotere groepen dan op eilanden met een natuurlijke vegetatie, waar gepaarde ganzen zich overdag vaak zelfs afzonderen van de groepen (Fig. 5). De effectieve foerageertijd van deze afzonderlijke paren wordt hierdoor verkleind (Tabel 1). Op de eilanden met gecultiveerd grasland wordt minder tijd aan foerageren besteed en meer tijd aan rusten dan op de eilanden met natuurlijke vegetaties (Fig. 6). Het dieet bestaat op de eilanden met gecultiveerd grasland vooral uit timotheegras (Fig. 7), waarvan het eiwitgehalte hoger is (Tabel 2) dan van beemdgras (*Poa*) en rood zwenkgras (*Festuca*), dat vooral op de eilanden met natuurlijke vegetaties wordt gegeten. Bovendien groeit timotheegras sneller dan de andere grassoorten (Fig. 8).

Op de Noorse eilanden treedt een snel herstel op van de conditie van de ganzen (Fig. 9). Op de eilanden met gecultiveerd grasland blijken de ganzen ongeveer drie dagen eerder dan op de andere eilanden de juiste conditie bereikt te hebben om weg te trekken. Dat verschil is waarschijnlijk de oorzaak van de gevonden verschillen in het voortplantingssucces. Van de ganzen die op de eilanden met gecultiveerd grasland pleisterden keerde in 1988 ruim 18% in Schotland terug met jongen, terwijl van de ganzen die op eilanden met een natuurlijke vegetatie pleisterden nog geen 10% met jongen terugkeerde (Tabel 3).