# Abdominal profiles of Barnacle Geese Branta leucopsis at staging areas in Iceland in May

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The abdominal profiles of Barnacle Geese (Branta leucopsis) staging in northwest Iceland in spring were studied from 13-18 May 1978 and 25 April-10 May 1999 and on Islay, Scotland from 12-15 April 1979. Mean profile scores were highest in April 1979 and mid-May 1978. In 1999, the profile scores were lowest on 25-26 April. Mean daily rates of increase in the profiles of both sexes were greater between 26 April and 4 May than between 4 and 9 May. Fatter females tended to be paired to fatter males and fatter juveniles had fatter parents. Pairs still accompanied by young were fatter than most other pairs, which were usually fatter than single adults or juveniles. Differences in profile frequencies between districts were greatest on 25-26 April, soon after the geese had arrived: males and juveniles in small families were then in better condition than those with three or four young. On 4 and 9-10 May 1999, and 13-18 May 1978 there were no significant profile differences between members of small and larger families. Geese in the districts where they were thinnest initially fattened most rapidly.

Key Words: abdominal profile, Branta leucopsis, spring migration.

Previous studies of geese at spring staging areas in Iceland have included observations on the abdominal profiles (Owen 1981) of Pink-footed and Greenland White-fronted Geese, Anser brachyrhynchus and A. albifrons flavirostris (Boyd & Fox 1995; Boyd et al. 1998). The observations reported here were intended to obtain comparable information about the Greenland breeding Barnacle Geese that stage in north Iceland in spring (Ogilvie et al. 1999). Percival &

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Percival (1997) studied the feeding ecology of these geese in Iceland in 1987 and 1994; they recorded the profiles of ringed geese (Percival, Mitchell & Paynter 1987), but did not report them, nor assess the condition of large numbers of geese. Prop & Black (1998) studied the food intake, body reserves and subsequent breeding success of Svalbard breeding Barnacle Geese while using different habitats in spring staging areas in Helgeland, north Norway. They

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Figure 1. Distribution of main staging areas of Barnacle Geese in north Iceland (after Percival & Percival 1997)

recorded abdominal profiles, but combined those of females and males in reporting their results. Here, particular attention is paid to the differences between paired females and males.

34 Barnacle Goose spring profiles

## Methods

Abdominal profiles are good indicators of the fat reserves of migrating geese. Linear relationships between profile scores and total fat mass have been found for Pinkfooted Geese (Madsen et al. 1997), Greenland White-fronted Geese (A.D. Fox, pers. comm.) and Hawaiian Geese Branta sandvichensis (Zillich & Black (2000) in press). Recording of abdominal profiles is most reliable when the birds are at close range. In mid-May 1978, the geese were watched from a car at distances of 50-200m. In 1999, many geese were also feeding close to roads on 25-26 April, when snow-free areas were scarce. On 4 and 9 May the geese were more wary,

especially in areas where much illegal shooting of geese had occurred. On all occasions the proportion of individuals in a flock whose profiles could be clearly seen varied greatly. Care was taken to wait until individuals were broadside on to the observer and with their heads down (Owen 1981). A seven-point scoring system was used in all three years; in 1978 and 1979 adapted from Owen's four-point scale, in 1999 from Madsen (1995). Paired birds were concentrated on with females identified by their behaviour as well as their generally smaller size. When walking, females feed nearly continuously, while males spend much time with their heads up, guarding their mates from rivals and from possible predators. Most Barnacle Geese less than a year old still show some juvenile plumage in April and May and, when in family groups, are often perceptibly smaller than their parents. Identifying family groups is sometimes complicated by the presence of additional adults, perhaps progeny from previous

years. No attempt was made to identify the sex of juveniles or of apparently unpaired adults. A few records of adult trios and other anomalous groups have been omitted. It was assumed that an ordinal relationship between profile scores and fat mass exists for Barnacle Geese, as for the other species noted above, so that the distributions of class scores can be summarized by their means and standard deviations. For statistical testing,  $\gamma^2$  tests of the full distributions are sometimes more useful. Percival & Percival (1997) grouped their observations on Barnacle Goose ecology in north Iceland in 1987 and 1994 into 22 localities, in four districts (Figure 1). The profile samples have been grouped into those four districts for some analyses.

Icelandic weather records for 1999 have not yet been published. Those for the years 1970-1998, published in *Vedrattan*, the journal of record of Vedurstofu Islands, provide a useful background.

## Results

## Phenology

Most Greenland breeding Barnacle Geese leave northwest Scotland in the second half of April: mean 19 April (n=32, s.d. 9.4), largest numbers 27 April-1 May (Boyd, Bell & Watson, in press). They left Islay over the period 21-26 April in 1987 and 20-28 April in 1994 (Percival & Percival 1994). The mean date of first sightings at weather stations in Iceland since 1980 has been 22 April (n=13, s.d. eight days). In 1999 at least 130 were seen at two sites near Hvanneyri, west Iceland on 21 April, and 10 on 22 April, but none there later. Apart from a record from south Iceland on 25 March and another 'in April', the mean date of 26 spring recoveries of ringed geese in north Iceland is 12 May (s.d. nine days), range 3 May-8 June (from listings in Dansk Ornithologisk Forenings Tidsskrift). In the 1970s, most departures occurred around 20 May (A.Gardarsson, pers.comm.). In both 1987 and 1994, the first departures were seen on 16 May and most had left by 18 May, giving a length of stay at this staging area of about 25 days (Percival & Percival 1994). By analogy with other transient geese (see below), most individuals do not remain for the entire period. Arrival at the breeding grounds usually occurs 20-23 May, laying beginning within a few days (Salomonsen 1967). There are few detailed records of the start of incubation. Assuming an incubation period of 24-25 days and a mean clutch of four (Ogilvie 1978), backdating of 12 nests where hatching was seen in 1987 (Cabot, Goodwillie & Viney 1988) suggests that laying began 29 May-3 June, 11-16 days after most geese had left Iceland.

## Profile changes in Iceland

The frequency distributions of profile scores of paired females and males on different dates in 1999 are shown in **Figure 2. Figure 3** shows the score distributions on Islay, 12-15 April 1979 and in Iceland, 13-18 May 1978. **Tables 1 and 2** compare the means and standard deviations of the sample scores of paired females and males, and of juveniles and other adults, in those periods.

The mean profile scores on Islay in mid-April 1979 were very similar to those in Iceland in mid-May 1978, although in mid-May the geese about to breed had well developed reproductive systems, which increase the abdominal profiles of mature females, more than those of males. The flight from Islay to north Iceland is longer (1,300 km) than that from Iceland to the breeding areas in east Greenland (600-900









Figure 2. Frequencies of abdominal profile scores of paired adult females and males on 25 April, 4 May and 9 May 1999.

		25/26 Ma			4 May			9/10 May	
	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.
Paired females	362	2.05	0.64	452	4.00	0.64	259	4.68	0.62
Paired males	362	1.90	0.50	452	3.30	0.66	259	3.79	0.54
Other adults	30	1.66	0.48	16	3.18	0.78	16	3.50	0.58
Juveniles	115	1.60	0.43	236	2.88	0.46	68	3.08	0.38
Mean daily gain	2	5 Apr - 4	Hay -	9 May		Tota	al Increa		
in score		9 days	5 d	ays		init	ial mea	— % n	
Paired females		0.167	0.0	76			87.2		
Paired males		0.156	0.0	98			99.5		
		0.169	0.0	64			110.8		
Other adults									

Table 1. Mean abdominal profile scores of Barnacle Geese in north Iceland, 25 April-10 May 1999

 Table 2.
 Abdominal profiles of paired and juvenile Barnacle Geese on Islay, 12-15 April 1979 and in north Iceland, 13-17 May 1978

Profile Score	1	2	3	4	5	6	7	Total	mean	s.d.
Islay - April 1979										
Paired females		2	30	59	53	28	2	174	4.47	1.03
Paired males	T	5	82	63	21	2	-	174	3.60	0.80
Juveniles	-	5	23	13	-	-	-	41	3.21	0.64
Iceland - May 197	8									
Paired females	-	-	42	51	58	17	8	176	4.42	1.09
Paired males	-	3	85	64	22	2	-	174	3.63	0.77
Single adults	-	5	3	I	-	-	-	9	2.56	0.73
								30	3.10	0.55



Figure 3. Frequencies of abdominal profiles scores of paired adult females and males on Islay, Scotland, in mid-April 1979 and in north Iceland, mid-May 1978.

km), so that larger stores of energy are needed for the first flight.

The mean scores of paired females were greater than those of paired males on all occasions. In 1999, the mean profile scores of both sexes increased more rapidly from 26 April to 4 May than from 4 May to 9 May. Juveniles and 'other adults' (those not obviously paired) tended to have lower profiles than members of pairs and to increase their profiles less. Mature pairs need additional reserves to enable males to occupy and defend breeding sites, while nesting females, which incubate almost continuously, largely depend on reserves built up in Iceland. Juveniles (9-10 months old) and other geese not yet ready to breed, need only to acquire sufficient energy reserves for the second leg of their migration, and can also delay their departure, to run less risk of arriving in east Greenland while the lowland areas remain snow-covered. Salomonsen (1967) noted that non-breeders arrive late in Greenland.

The drops in profile scores from

Date	Adult Profile scores	Juv	enile Pr	ofile S	cores	$\chi^2$	Р
Female Parer 25-26 April	nts I+2 3+4 Total	1 <b>46</b> 5 51	2+3 29 <b>38</b> 67	4+5 - -	Total 75 43 118	25.53	<0.001
4 May	2+3 4 5+6 Total	2 1 <b>7</b> 23 3 43	3 29 72 47 148	4    8  6 35	Total 47 113 66 226	23.82	<0.001
9-10 May	3+4 5 6 Total		2+3 21 30 13 64	4+5 <i>I</i> 6 <b>I0</b> 17	Total 22 36 23 81	11.08	<0.005
Male Parents 25-26 April	+2 3+4 Total	 49   50	2+3 54 14 68	4+5 - -	Total 103 15 118	7.38	<0.005
4 May	2+3 4+5 Total		2+3 120 76 196	4 6 <b>30</b> 36	Total 126 106 232	22.57	<0.001
9-10 May	2+3 4+5 Total		4 48 62	0 28 28	14 76 90	7.51	<0.005

**Table 4.** Comparisons of abdominal profiles of juvenile Barnacle Geese in families to those of their parents. Iceland, 25 April-10 May 1999. Numbers in bold are above and those in italic below, expected frequencies.

Scotland in mid-April 1979 to Iceland in late April 1999 are indicative of the use of fat reserves during a flight of about 1300 km. As the observations were made many years apart, they cannot be used to estimate the relative amounts of fat used by different classes of geese. Studies of Svalbard-breeding Barnacle Geese (Owen 1987) have shown that there are substantial interannual variations in the median profile scores of geese shortly before leaving the Solway Firth and at their main staging area on the Norwegian coast.

# Profile differences between pairs with and without broods

On Islay in mid-April 1979, profiles of only 18 pairs with broods were scored. The mean score of the females was 4.11 (s.d. 0.96), of the males 3.44 (s.d. 0.51). The corresponding scores of 153 pairs without young were 4.45 (s.d. 1.07) for females and 3.69 (s.d. 0.84) for males.

In 1999, the differences between the sexes and between pairs with and without broods were less on 25 April than on 4 or 9-10 May (Table 3). On 25-26 April, pairs with broods formed 21.0% of the sample. On 4 May (pairs with broods 29.6 %), the distribution of female profiles was similar for those with and without broods; but males with broods included significantly fewer with profiles of only 2 (10/134, 7.5 %) than those without broods (60/318, 18.9 %). Females with profiles of 3 made up only 6.5 % of the sample. On 9 May, both sexes showed significant differences between the profiles of those with and without broods: there were more scores of 6 and fewer of 4 among females with broods than among those without ( $\chi^2$ 

16.57, P<0.001). Only 20.4 % of males with broods had profile scores as low as 3, while 42.0% of those without young had scores of 2 or 3 ( $\chi^2$  8.89, P< 0.025). In mid-May 1978, the mean profile score of 14 paired females with broods was 4.22 (s.d. 1.06), that of 115 without broods 4.59 (s.d. 1.06). The mean profile score of paired males with broods was 3.67 (s.d. 0.77), the same as for those without young, 3.66 (s.d. 0.82). The proportion of pairs with broods was much lower in the profile samples in April 1979 (9.2 %) and mid-May 1978 (10.5 %), than in 1999 (26.4%). Sampling was opportunistic in all three years, though deliberately biased in favour of mated pairs. Some of the disparity may be related to differences in breeding success in the previous summers. Autumn flocks on Islay included only 4.9% juveniles (mean brood size 1.76) in 1977, 12.0% juveniles (mean brood 2.0) in 1978 and 12.8% juveniles (mean brood 2.3) in 1998. The scarcity of family groups in mid-May 1978 might have been due in part to earlier emigration by pairs with families. The differences between the profile scores of females and males are much greater than the

District	% on improved grass	n	Females n mean s.d.		Males mean s.d.				
A-Hunavatn	67.5	71	4,25	1.05	3.68	0.63			
Skagastrond	61.3	60	4.37	1.09	3.68	0.83			
Skagafjordur	20.2	7	4.14	1.07	3.43	0.79			

Table 5. Mean abdominal profile scores of paired Barnacle Geese in different districts in May 1978.

District	F	aired Fem	nales	Pa	aired Males		
	25-26	4	9-10	25-26	4	9-10	
	April	May	May	April	May	May	
V-Hunavatn	1.29	3.80	4.92	1.29	2.94	4.08	
	(7)	(51)	(24)				
A-Hunavatn	2.71	4.10	4.60	2.09	3.34	3.70	
	(182)	(258)	(161)		3.8		
Skagata	2.12	3.57	-	1.63	2.90	-	
	(82)	(21)					
Skagafjordur	2.55	4.05	4.74	1.81	3.33	3.89	
•	(91)	(122)	(73)				
Mean Increase	26 Apr-4 M	lay	4-9 May	26	Apr-4May	4-9 May	
V-Hunavatn	2.52		1.11		1.66	1.14	
A-Hunavatn	1.39		0.50		1.20	0.35	
Skagata	1.45		-		1.27	-	
Skagafjordur	1.50		0.69		1.52	0.55	
Total increase %							
Initial mean							
V-Hunavatn	281.4				216.3		
A-Hunavatn	69.7				77.0		
Skagafjordur	85.9				14.9		

**Table 6**. Mean abdominal profile scores of paired Barnacle Geese in districts in northwest Iceland on different dates in 1999. Sample sizes in parenthese below female means.

differences within each sex between parents and pairs without young. The large differences between females and males on 9 May 1999 (female mean score 4.68, male 3.79) and 13-18 May 1978 (females 4.49, males 3.72) presumably reflect both the much greater enlargement of the reproductive system of females and their need to bring substantial reserves to the nesting areas, to help them survive the period of incubation.

In mid-May 1978, many completed copulations were seen, suggesting that both sexes were then in breeding condition. Though pre-copulatory displays were seen on 9 May 1999, none led to copulation.

In years when snowmelt is early, the geese may be able to feed intensively in Greenland before beginning to lay. This seems not to have been reported, but those breeding in Svalbard feed for a week or more in the south of the main island before moving to their breeding sites (Tombre et al. 1996).

# Profiles of parents and their offspring

Fatter pairs had fatter young. **Table 4**, which includes groupings of two or more score classes to provide adequate samples, shows that, for both female and male

parents, departures from the expected frequencies were greatest in the highest and lowest classes. Correlation coefficients suggest that juvenile condition may be tied rather more closely to that of the male than the female parent: r=0.89 and r=0.87 respectively; after partialling out the other sex, the corresponding coefficients are 0.706 and 0.627 (P< 0.05 in each case).

The sizes of the broods accompanying parents can be affected by: (1) rearing success in the previous summer, (2) winter survival of juveniles and (3) the success of the family in making the flight from Scotland to Iceland together. Family cohesion, often weak in midwinter, is sometimes re-established prior to the spring migration (Black & Owen 1988,1989; Owen & Black 1988, pers.obs.). In most years, relatively few pairs of Greenland-breeding Barnacle Geese succeed in bringing young to wintering areas, as losses of goslings to Arctic foxes and other predators are heavy (Cabot et al. 1984, 1988; Ogilvie et al. 1999).

It might be expected that families with most young would be attached to the males in best condition. On 25 April 1999, the opposite seemed to be true: 69 males with broods of 1 or 2 had a mean profile score of 1.99 (±0.61), while 7 with broods of 3 or 4 had a mean of 1.43 (±0.53). On 4 May the situation had been reversed: 105 males with 1 or 2 young had a mean profile score of 3.44 (±0.65), 19 with 3 or 4 a mean of 3.21 (±0.86). On 9 May, 53 males with I or 2 young had a mean score of 4.08 (±0.58); 2 males each with 3 young both had profiles of 3. The corresponding means for females with young (same sample sizes) were: 25 April, with 1 or 2 young, 2.38 (±0.73), 3-4 young 2.86 (±0.45); 4 May, I-2 young 4.12 (±1.05), 3-4 young 4.14 (±0.64); and 9 May, 1-2 young, 4.93 (±0.89), two with 3 young 5.50 (±0.71). In mid-May 1978, there were no significant associations between brood size and the profile of either parent. (The method of recording in April 1979 precludes a test of this point).

Brood size affected the profiles of the young on 25 April 1999: broods of I had a mean profile of I.84 ( $\pm$ 0.47, n=45) and those of 2-4 a mean of I.54 ( $\pm$ 0.57, n=83). There were no significant differences between brood-size profile means on the later visits.

### **Differences between Districts**

In 1978, about a third of all feeding by geese was on rough grass and river banks. Dropping analysis showed that Poa and Calamagrostis were the principal plants taken (A.Gardarsson, pers. comm.). The latter genus is found in natural wetlands. not in improved grasslands. Some geese were found in nearly all the localities where they were later found by Percival & Percival (1997); Austur-Hunavatn held 7,900 of 16,700 Barnacle Geese seen during an aerial survey on 15 May 1978 (A. Gardarsson and pers. obs.). Though there were nearly as many geese in Vestur-Hunavatn, none could be approached closely enough to obtain abdominal profile scores. Table 5 summarises the mean profile scores in the other three districts. The sample from Skagafjordur was small, but the low mean scores may be associated with the scarcity of geese in that district in mid-May 1978. From 13-14 May to 16-18 May, the mean scores of paired females rose in Skagastrond (the west coast of Skagata) and fell in Austur-Hunavatn. The scores of paired males in Austur-Hunavatn did not change, while those in Skagastrond fell.

In 1999 the geese fed almost entirely on improved grasslands, as they had done in 1987 and 1994 (Percival & Percival 1997).

District	(west) Hunavatn	Skagata	Skagafjord	(east) Eyjafjord
Station	Blonduos	Hraun	Berg. Holar Naut.	Akureyri
Height a.s.l.	23	3	43 160 115	23
Daily	4.6	3.8	5.04.95.1(1.8)(1.8)(1.7)5.15.55.5	6.3
Temp (C)	(1.6)	(1.7)		(2.2)
1978	5.7	5.3		6.8
Precipitation	29	26	212823(18)(25)(10)345950	26
Total (mm)	(23)	(18)		(15)
1978	52	41		29
Wind Speed	3.5	5.0	6.52.64.8(1.0)(1.0)(1.0)4.21.64.6	4.4
(m/s)	(0.7)	(0.9)		(0.8)
1978	3.7	3.9		4.0
Last Total	30 Apr	7 May	2 May 14 May 14 May	25 Apr
Snow cover	(12.4)	(12.4)	(16.03) (17.6) (21.7)	(15.3)
1978	29 Apr	30 Apr	1 May 23 Jun 13 May	16 Apr
% Snow cover	7.3	2.8	2.4  8.8 9.9	7.9
in May	(10.3)	(9.8)	( 4.2) ( 5.2) ( 2.8)	(11.0)
1978	-	-	-  5 6	-

**Table 7.** Mean weather conditions in May in different districts of north Iceland used by Barnacle Geese in Spring 1970-1998. Standard deviations in parentheses. Data for 1999 not available.

Most of those seen on river banks and wet meadows were resting, bathing or drinking, not feeding. There were substantial differences between the profiles of geese in the four districts (Table 6), presumably due to frequency of disturbance as well as to variations in the quality and abundance of food. The low scores in the west on 25 April were probably those of geese that had arrived very recently; no geese were seen on those farms on later visits. Further east, the district means were markedly higher, while differing from each other. Birds in Vestur-Hunavatn and at sites along the west and east coasts of Skagata continued to have lower mean scores than those in Austur-Hunavatn and Skagafjordur, which held most of the geese. Though the geese in Skagafjordur were more difficult to approach, probably because they had been shot at more often than those further west, they showed greater mean gains than those in Austur-Hunavatn. This suggests that in 1999, unlike 1978, the abundance and/or quality of available food may have been higher in Skagafjordur than further west.

### Local Climates

In this context the climatic differences within and between the districts are of interest (**Table 7**). From 1970 to 1998 there were no sustained trends in local temperature or precipitation in May, though there were wide variations in the date of last complete snow cover, between stations and within and between years.

'Beginning of vegetation' (mean 6 May,  $\pm 12$  days) at Barkarstadir (114 m a.s.l.) was delayed in years when mean temperatures in April (0.0° C, +/- 1.5), May (4.1° C, +/-1.7) and April+May (2.0° C, +/- 1.7) were low (n=23): r=-0.702, r=-0.648, r=-0.854 respectively (all P< 0.001). In 1978, growth at Barkastadir was reported as not starting until 1 June, despite above average temperatures in May.

The differences between the local period mean temperatures in October-March (the winter period in Iceland) and in April and May are enough to have substantial effects on the yields and standing crops of grasses, on both improved and unfertilized lands (Fridriksson 1972, and pers. comm.), as well as on the start of new growth.

In the areas used by the geese, the mean date of last complete snow-cover was earlier near the sea than inland. In 1999. the geese moved up the Skagafjordur valley as the season progressed. They were then competing with Pink-footed Geese, though the latter made heavy use of three unploughed stubble fields, in which few Barnacle Geese were seen. The north end of the exposed peninsula of Skagata was cool and foggy, when not windy, yet it was used persistently by Barnacle Geese, though less heavily than the larger grass fields on the west side. The north has the advantage of very little disturbance by passing traffic.

The only weather records for Vestur-Hunavatn are from Hjaltabakki (1970-1980) and Blonduos (1981-1998), both near the coast, so that the impression given by **Table 7** that this district is warmer than those further east is misleading. In 1999 the geese in Vestur-Hunavatn first fed close to the coast, moving inland as soon as snow clearance permitted.

In summary, many of the movements of

the geese during their stay in north Iceland, which are not the results of disturbance, are probably related to local phenological differences, enabling the geese to follow the 'early bite' from fields near the coast to inland sites, where the start of grass growth may be 4-10 days later. In mid-May 1978 the geese continued to feed on both improved and rough grass: 42 % of those seen on 13-14 May, and 79 % of those on 16-17 May, were on improved grass. In 1999, there was no obvious shift away from improved grass, as reported from Norway by Prop & Black (1998), though this might be due to the observations ending as early as 10 May, a week or more before the likely departure date.

# Discussion

The nutritional needs of different age and sex classes of geese in spring staging areas are not identical. When food resources in spring staging areas are scarce, pairs accompanied by young should have an advantage, as family units readily displace pairs without young. The simulation model used by Lang et al. (1998) to study spring staging of Barnacle Geese in Norway assumes 'a despotic distribution' of geese foraging on small patches of vegetation, with the best competitors foraging on the patches providing the highest daily intake and biomass. That model may well be appropriate when the geese are dispersed in small groups on scattered patches of vegetation, as is the case in Helgeland. Norway. In north Iceland, most of the geese were feeding in relatively large groups, especially in 1999, and did not seem to be behaving in the prescribed way.

Most of the findings reported here are consistent with those from previous

observations on Pink-footed and Greenland White-fronted Geese staging in Iceland in spring (Boyd & Fox 1995; Boyd *et al.* 1998), with observations on the Pinkfooted Geese present in Skagafjordur in 1999, and with published accounts of Barnacle Geese staging in Norway (Owen 1987; Prop & Black 1998).

The observations in 1978 support those on White-fronted Geese, which suggested that many geese may start the final leg of their spring migration carrying relatively little abdominal fat. The flight of the Barnacle Geese to east Greenland (400-900 km) is less demanding than that faced by the White-fronted Geese, which have to cross the Greenland icecap on their way to breeding areas along the west coast.We had initially supposed that, among mature females in particular, there might be some condition threshold (whether minimum or be reached maximum) to before departure. That does not seem to be the case. The spread of scores suggest that geese may be 'satisficers' (Simon 1982), rather than 'optimisers' or 'maximisers': they do as well as possible to achieve certain condition levels and gradually adjust these upwards or downwards, depending on whether outcomes exceed or fall short of the original target. There are energetic costs of flying with a heavy fat load, and additional risks in leaving with lower loads.

In their studies in north Norway, Owen & Gullestad (1984) and Prop & Black (1998) were interested chiefly in the aggregate relationships between the geese and the food resources available to them. Prop & Black (*loc.cit.*) found that from 30 April to 5 May, geese using agricultural land in Norway had lower mean profile scores than those on islands. After 14 May, those on agricultural land had the highest mean scores. They suggest that the rate of increase in profile scores in Norway slackened after 12 May, reflecting a shift from the acquisition of fat to protein. The lower rates of change in profile scores after 4 May suggest that a similar shift may have been occurring in Iceland in 1999.

Fox & Gitay (1991) showed that the breeding success of Barnacle Geese in Greenland was linked statistically with meteorological variables in Scotland in April (wind direction, state of ground, precipitation), and with snow cover and precipitation in Greenland in May, as well as with weather conditions in north Iceland (at Nautabu) in the second half of April and first half of May. The field studies in Iceland have shown that the recovery of Barnacle Geese from their first migratory flight and their preparations for moving to east Greenland can be influenced by many Iocal events.

Geese show great skill in selecting the best available food sources at the microtopographical level of grass tussocks (Kristiansen et al. 1998). They seem as skilled in selecting feeding sites, as smallscale phenological differences create new opportunities. Until the second half of the Twentieth Century Barnacle Geese in their spring staging areas must have been almost wholly dependent on 'natural' grasslands, whether on islands and saltmarshes in Norway or river-banks in Iceland.Yet the shift from feeding on rough grass to improved grasslands that seems to have been completed in Iceland between 1978 and 1987 (cf. Percival & Percival 1997) does not seem to have altered the spread of profile scores within each age and sex class near the time of departure.

It will be interesting to see whether other observers using the same procedures over many years will obtain consistent results. It should not simply be assumed that observations made many

years apart cannot be compared. Longitudinal studies of changes in body condition, including the use of abdominal profiles, could prove as useful as those of changes in morphology over time (Boyd & Berry 1996; Przybylo et al. 2000) in studying phenotypic plasticity.

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