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CHANGES IN ABDOMINAL PROFILES OF GREENLAND WHITE-FRONTED GEESE DURING SPRING STAGING IN ICELAND

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Abdominal profiles of spring-staging White-fronted Geese in Iceland were recorded in 1990, 1991, 1997 and 1998, chiefly at Hvanneyri, the largest known staging area. Median profile scores were markedly lower on arrival in Iceland than at departure from Ireland in the same spring. Median profile scores and the proportions of fat geese increased from arrival (16-24 April) to departure (by 12 May), though profiles of some individually-marked birds did not increase. Most of the increase in median scores in 1997 and 1998 occurred before the end of April, whereas most occurred after that time in 1990 and 1991. Median scores in mid-April were generally higher in 1990 and 1991 than in 1997 or 1998, but those in May were higher in 1997 and 1998 than in 1990 and 1991. Median scores from paired females started higher than males and increased more rapidly and pairs with broods tended to have larger profiles than those without. In 1998, other adults, confirmed or presumed to be offspring from earlier years, accompanied about 5% of pairs. These pairs, and the 'adults' accompanying them, also tended to have larger profiles than pairs without young. The median profile scores of females feeding on swards dominated by Meadow-grass Poa pratensis increased more rapidly than those on Tufted hair-grass Deschampsia caespitosa, though those of males did not. Many geese apparently left for west Greenland with relatively little abdominal fat.

Introduction

Greenland White-fronted Geese *Anser albifrons flavirostris* breed in west Greenland and winter in Ireland and western Scotland (**Figure 1**). The coastal lowlands of south-west and west Iceland provide important spring staging areas for these geese, after the 1000-1500 km flight from their winter quarters. After a stay of 2-4 weeks in Iceland, the geese fly on to west Greenland, a flight of at least 1400 km, involving crossing the extensive and high (> 2500 m) inland icecap. During their stay in Iceland they must recoup energy stores used during the first flight and accumulate sufficient stores for the second. These requirements suggest that the

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geese are likely to appear fatter (based on the visual assessment of abdominal fat stores by Owen 1981) before their departure from Ireland than on their arrival in Iceland, and to fatten again before they move on. We aimed to see how quickly, and to what extent, the geese in Iceland in spring changed their appearance, individually and collectively, and to assess what factors may affect this process.

Methods

We used Owen's (1981) technique of matching the perceived shape of the underparts of Barnacle Geese *Branta leucopsis* in the field against standard outlines of the 'abdominal profiles' of geese, seen in side view. This technique is used to assess the amount of abdominal fat stores the geese are carrying and the state of their reproductive systems. The advantages and limitations of using abdominal profiles - hereafter referred to as 'profiles' - to track changes in the internal condition of geese have been discussed elsewhere (Owen 1981, Gauthier *et al.* 1984, Boyd & Fox 1995).

Madsen (1995) introduced a set of seven standard outlines of Pink-footed Geese *Anser brachyrhynchus*, which Boyd used in 1997 and 1998. The other observers continued to use Owen's standard images. This should have helped to ensure that their 1997 observations were comparable with those made in 1990 and 1991. The two sets of standards are unlikely to result in very different assessments.

As the rating systems are ordinal, not scalar, the propriety of using means and standard errors of the scores to summarise their distributions is in doubt. However, Fox *et al.* (1998a) found a linear relationship between profile score and goose body mass and Madsen (unpublished data) found a similar relationship in Pink-footed Geese. Here, as advocated by Owen (1981), median scores are used instead of means, the significance of differences between medians was tested using Moods Median Tests (Siegel 1956).

The observations of profiles (scored to the nearest 0.5 after Black *et al.* 1991) in winter used here were all made by Walsh, at the Wexford Wildfowl Reserve in south-east Ireland, by sampling profiles of collared birds only. Scan sampling (using the same scoring system) of unmarked individuals was also carried out by him and other observers in Iceland in 1990, 1991, 1997 and 1998. Though ignoring the sex, age and family status of

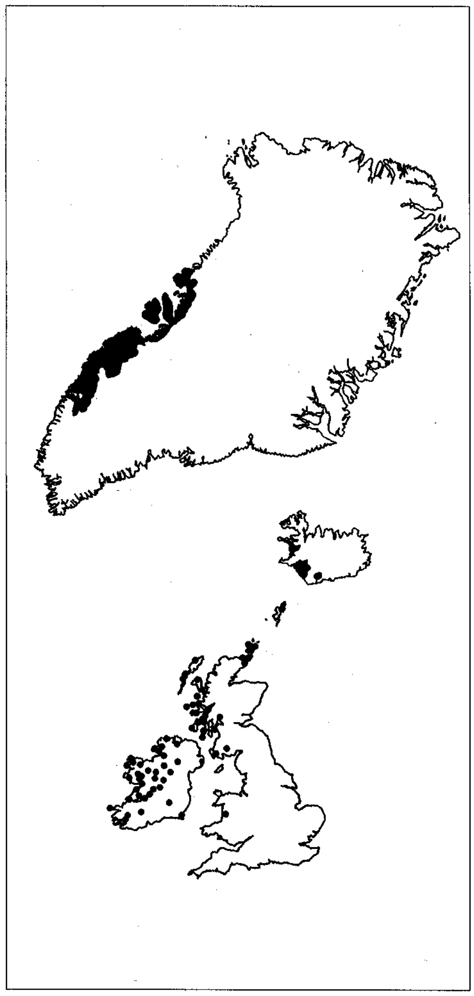

Figure 1. Map showing approximate breeding range of the Greenland White-fronted Goose in west Greenland (dark shading, but note that birds are also known to summer further north), staging areas in west and south Iceland (dark shading) and regularly used wintering areas in Ireland and Britain (dots).

individuals loses useful information, scan sampling is a quick method of assessing the profiles of large numbers of geese.

Boyd collected most of the profiles of females and males in clearly mated pairs, in all four years. He identified males by their stockier heads and necks, usually a larger size and more frequent use of the head-up position, females being preoccupied with feeding, except when disturbed. He used Owen's standard images in 1990 and 1991 and Madsen's in 1997 and 1998.

An alternative way of looking at differences between the scores of paired females and males is to compare the changes in the extremes of their frequency distributions, rather than their median scores. The reproductive system enlarges in spring much more in mature females than in males (for which there were few scores of 5 using the Madsen 1995 scale). A score of 4 or more is used to define a 'fat' male, while females need to score 5 or more to qualify. Even when the grouping of scores is biased in this way, 'fat' males remain much scarcer than 'fat' females. For both sexes, 'thin' birds are those with scores of 1 or 2.

The principal data were collected on, or close to, the farm attached to the agricultural college Baendaskólinn á Hvanneyri, Borgarfjardarsysla (64°34'N, 21°46'W) from 17 April to 11 May 1997 and 18 April to 8 May 1998. Supplementary observations were made in adjacent parts of Borgarfjördur and in Myrar to the north and west, principally at two sites c.18 km west and c.25 km north north west of Hvanneyri during 1997 and 1998. Other records were made at Hvanneyri by Walsh from 2-7 May 1990 and by him and others in south-west Iceland in the springs of 1990 and 1991, near Fljotsholar, Flói (63°47'N, 20°49'W), close to the coast, and along a 40 km road transect inland in Skeid (64°07'N, 20°32'W, see **Figure 2**).

In addition to standard metal tarsal rings, in the springs of 1997 and 1998 over 400 Greenland White-fronted Geese were carrying plastic collars and leg rings with readable combinations of letters and numbers, so that they could be identified individually at a distance. They have been marked in west Greenland in summer and Wexford in winter. Fifty different collared birds were seen in spring 1997 and 53 in 1998, 18 being seen in both years.

Most of the fields on the college farm at Hvanneyri consist of grass. Apart from a few experimental plots, few fields have been reseeded recently, so that the original dominant grass has in most cases been invaded by native species. It is possible to classify the sward in most fields as predominantly of one, or two, grass species. Using notes made in 1997 and 1998, two questions are addressed here: (1) were there substantial differences in the profile scores of geese feeding on different swards? (2) did any differences become more or less apparent in May, while the geese were leaving?

Poa pratensis was dominant in the largest number of the 57 classified fields, *Deschampsia caespitosa* was next most abundant, and with mixtures of the two forming the third most frequent category. The rankings by area are the same, with *Poa* fields occupying 54.5% of the 83.9 ha included in the classified fields. In 1998 only three fields (6.9 ha) were dominated by Timothy-grass *Phleum pratense*; a fourth (1.72 ha), with a mixture of *Phleum* and *Poa*, was also

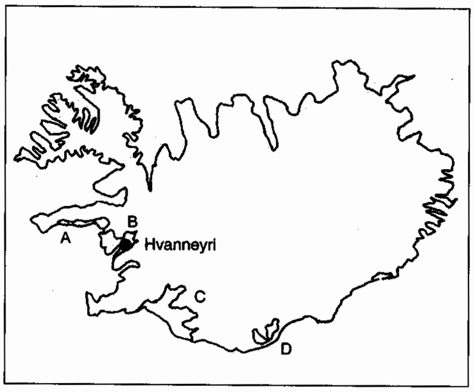

Figure 2. Major known staging areas of White-fronted Geese in Iceland, showing the location of the Hvanneyri Agricultural College study area in Borgarfjördur, west Iceland. A indicates southern side of Snaefellsnes, B Myrar, C staging areas in Ölfus, Flói, Holt and Landeyjar and D Álftaver and Medalland.

included in the sample. Extensive areas of rough grass, rarely used by the geese, can be ignored. The sedge (*Carex lyngbyei*) meadows near the shore were used intermittently, but the geese on them were too distant for their profiles to be rated.

Results

Differences in spring profiles between Ireland and Iceland

Median profile scores of geese in late March and April at the Wexford Wildfowl Reserve and from soon after their arrival in Iceland are shown in **Figure 3**. In 1991 and 1998, geese increased abdominal profile to the point of departure from Wexford, but in 1990 and 1997, geese departed from Wexford early, hence the period of rapid fat accumulation was not registered in April of those years. Geese arrived in Iceland with substantially lower median scores, and in all years, median scores increased during the staging period (**Figure 3**).

Profile changes in Iceland

The median scores from scan-sampling in south-west and west Iceland on different dates in 1991 and 1997 showed a general tendency to increase from arrival (Spearman Rank correlation of median score with date statistically significant in 1991, $r = 0.880$, $p < 0.02$ and 1997, $r = 0.924$, $p < 0.05$). In 1990, the median scores in the south-west peaked in early May, then fell shortly before the last geese left (7-11 May). At Hvanneyri, 2-7 May 1990, there was a much higher proportion of heavy birds than in the south-west, while the scores of those at Myrar, about 25 km north-west of Hvanneyri, on 9-11 May resembled those in the south-west at the same time. In 1998, data were only available from Hvanneyri, but a sustained increase through the staging period was observed there.

Changes in profiles of pairs

Pair sampling in the south-west was relatively infrequent in 1990 and 1991, so samples are small. However, the median profiles of females started higher than those of males and increased more rapidly (**Figure 4**). Expressing the mean daily rates of increase in median scores as percentages of the mean median for the entire period, the rates of increase in 1990 were 2.29% per day for females, 0.52% for males; in 1991 0.96% for females, 0.95% for males. Pair sampling in the west in 1997 and 1998 (**Figure 5**) was more intensive. In both years, most of the increases in profiles appeared to take place before the end of April. In both 1990 and 1991, females had higher median profiles than males (Moods Median test, chi-squared = 30.5, df = 1, $P < 0.001$ and chi-squared = 54.6, df = 1, $P < 0.001$, respectively). The same was true in 1997 (Moods Median test, chi-squared = 199.5, df = 1, $P < 0.001$) and 1998 (Moods Median test, chi-squared = 39.8, df = 1, $P < 0.001$). In 1997, the median female score increased daily at a mean rate of 1.78% and males by 1.30%, while in 1998, female scores increased by 2.21% and males by 1.72%. The median scores of both sexes were lower in 1998 than in 1997 (Moods Median tests, males chi-squared = 29.9, df = 1, $P < 0.001$, females males chi-squared = 56.7, df = 1, $P < 0.001$).

There were proportionately fewer thin, paired geese in 1997 (chi-squared = 4.68, df = 1, $P < 0.05$) and more fat birds in 1998 (chi-squared = 7.23, df = 1, $P < 0.01$, **Table 1**) amongst early arrivals compared to the proportion in all springs combined. In 1991, no 'fat' geese of either sex were recorded soon after arrival in Iceland, although the median score before leaving Ireland had been high. In all four years, the proportion of fat females was much higher in May than in the April samples, while many males remained thin, especially in 1991 and 1998. Only small samples were obtained after 7 May, as most of the geese had already left.

Profile differences between neighbouring areas

In 1998, two sets of pair-profile scores were obtained from Myrar, on 25 and 29 April. On 25 April, the median score of 71 females at Myrar

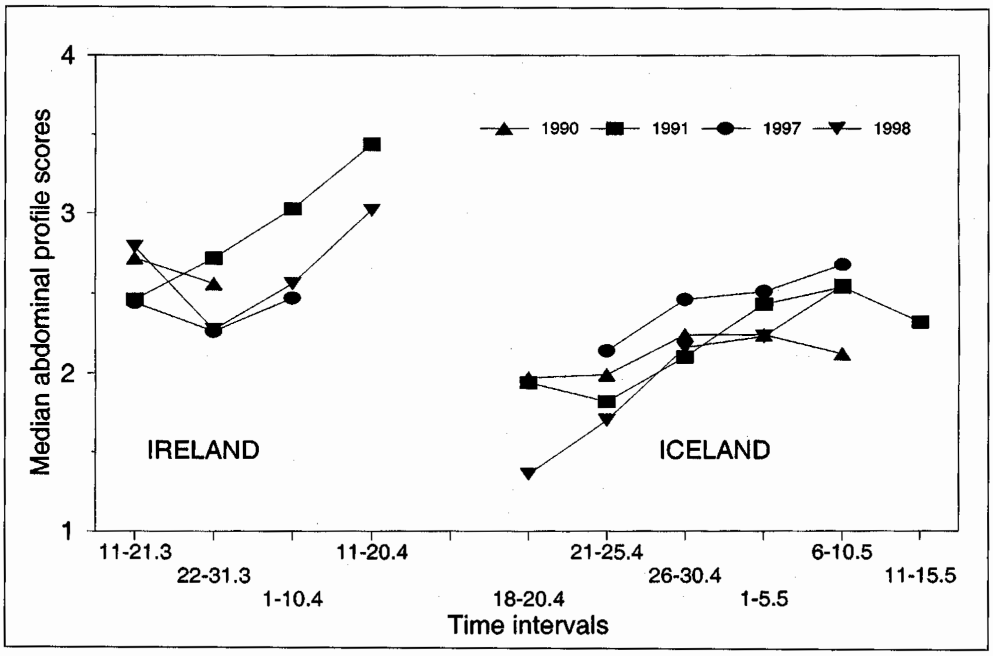

Figure 3. Median profile scores of geese (based on sampling intervals of 0.5) from spring sampling in Ireland and Iceland in 1990, 1991, 1997 and 1998.

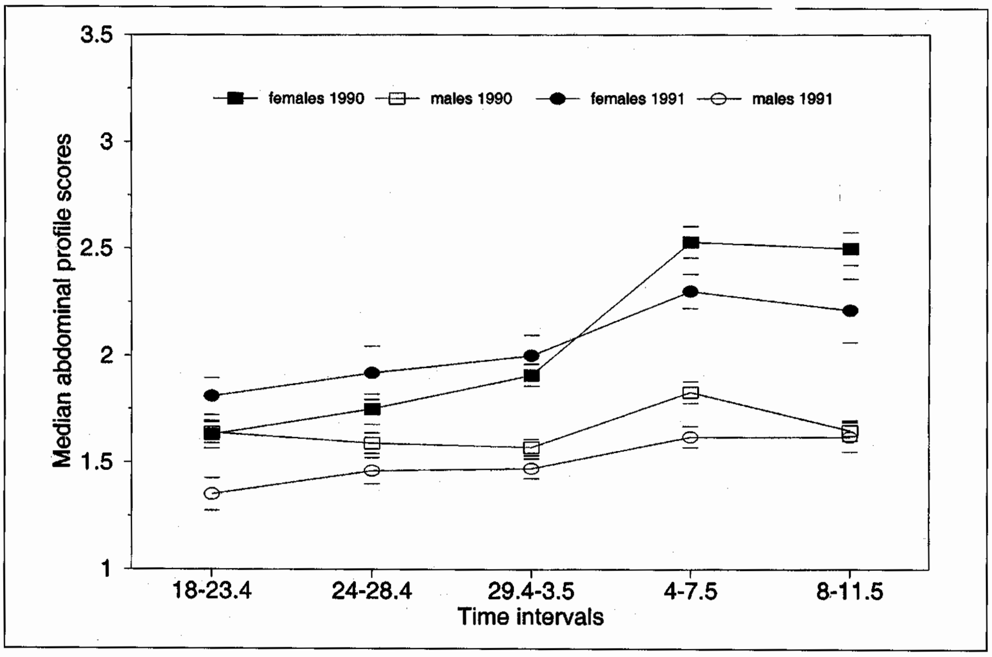

Figure 4. Median abdominal profile scores (± SE) of paired adult female and male geese in south-west Iceland in 1990 and 1991 (based on sampling intervals of 0.5).

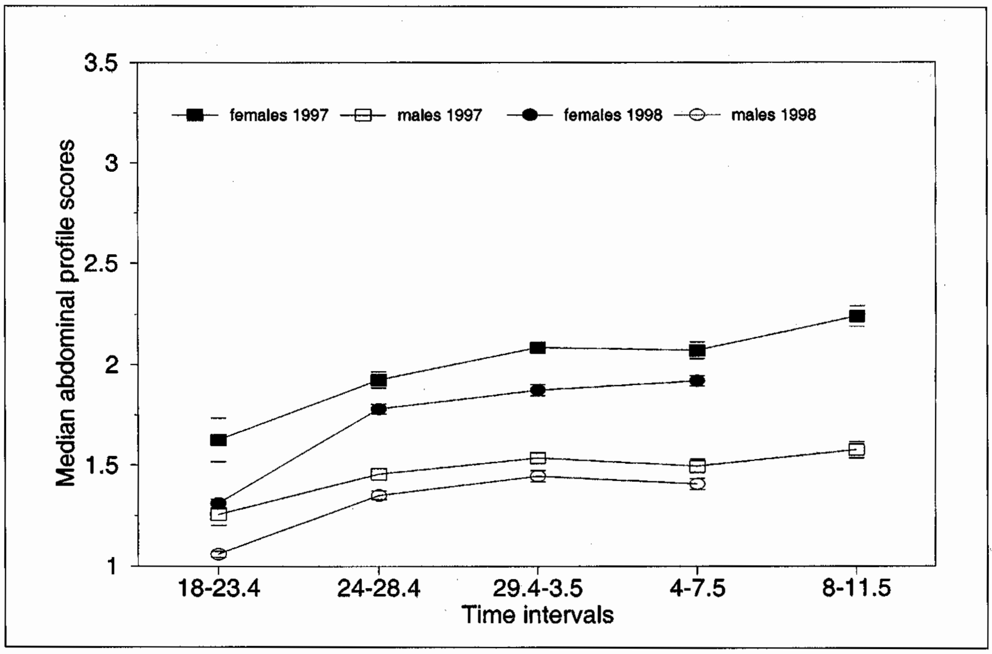

Figure 5. Median abdominal profile scores (± SE) of paired female and male geese at Hvanneyri in 1997 and 1998 (based on sampling intervals of 1.0, but corrected to 0.5).

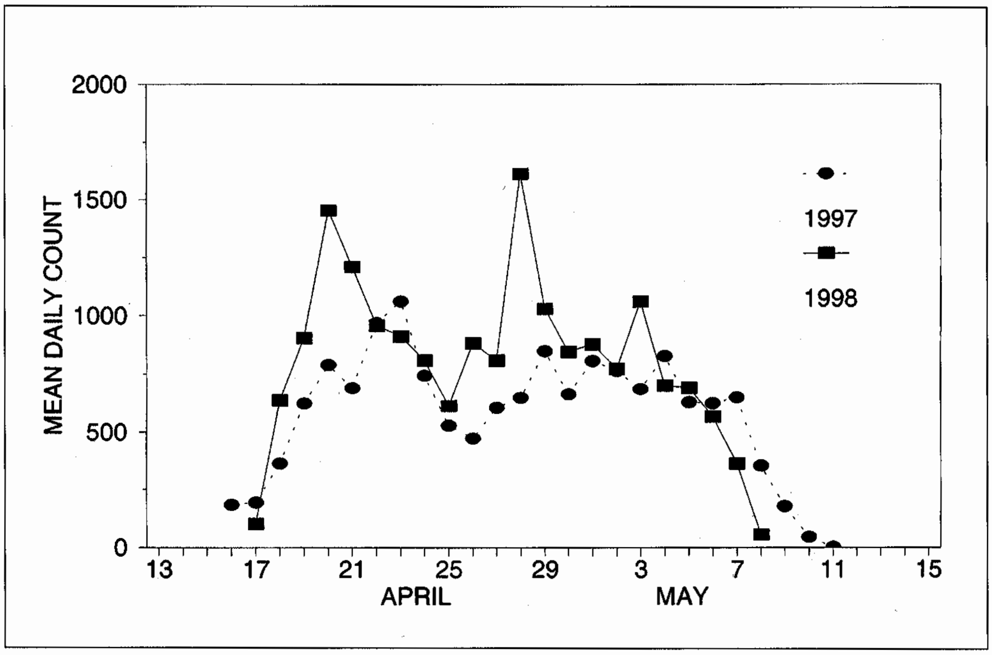

Figure 6. Daily counts of White-fronted Geese at Hvanneyri, 1997 and 1998.

Table 1. Percentages of adult female and male White-fronted Geese in clearly-mated pairs that were 'thin' and 'fat', early (19-22 April) and late (6-9 May) in their stay in Iceland in 1990, 1991, 1997 and 1998. 'thin' = 1 or 2(Madsen scale); 'fat'= 5(+) for females, 4 (+) for males. n = sample size, same for both sexes.

		females		males	
	n	thin	fat	thin	fat
Early					
1990	60	23.3	3.3	59.7	8.1
1991	32	37.5	0	85.7	0
1997	46	19.6	13.0	50.0	10.9
1998	253	47.0	0	79.8	0
mean		31.8	4.1	68.8	4.8
Late					
1990	68	7.4	30.9	48.5	7.4
1991	32	9.4	18.8	65.6	0
1997	120	0.8	29.2	30.0	17.5
1998	69	1.4	20.3	29.0	14.5
mean		4.8	24.8	43.3	9.8

(3.09) was not significantly different from that of 29 at Hvanneyri (3.15, Moods Median test, $P > 0.05$). On 29th, of 27 females at Myrar, the median score was 3.11 while that of 35 at Hvanneyri had increased to 3.73 (Moods Median test, $P < 0.05$). The median score of males was lower on 25 April at Myrar (2.01) than Hvanneyri (2.53, Moods Median test, $P < 0.05$), and had fallen further behind by 29th: Myrar 2.11, Hvanneyri 2.81 (Moods Median test, $P < 0.05$).

Scan-sampling in the two areas in earlier years also showed that geese (not sexed) in Myrar had statistically different median scores from those at Hvanneyri (Moods Median tests, $P < 0.05$). For example, In 1990, the median score on 9-10 May for 135 birds at Hvanneyri was 3.24, compared with 1.99 among 91 birds in Myrar.

Juvenile profiles

Few profiles of 10-month old geese were obtained in any year since attention was concentrated on adults. No attempts were made to identify the sex of 'yearling' geese, many of which lack obvious sexual characteristics in the field. Only four profiles of yearlings were recorded in 1991 and 35 in 1997. There were 142 records in 1990 and 167 in 1998 (**Table 2**). The striking difference between the two years was the presence in late April 1990 of 16 fat yearlings in a sample of 80, unmatched at any other time. The lack of fat juveniles in May 1990 suggests that families with fat young had moved on by the end of April.

Table 2. Frequency distributions and median scores [med.] of abdominal profiles of juvenile White-fronted Geese at different times during their stay in southwest Iceland in 1990 and at Hvanneyri in 1998 (units of 1.0).

period	1990								1998					
	n	1	2	3	4	5	6	med.	n	1	2	3	4	med.
18-23 Apr	15	-	3	5	7	-	-	(3.4)	45	2	38	5	-	2.05
24-29 Apr	80	3	12	23	26	12	4	3.59	53	5	45	3	-	1.99
30 Apr -3 May									41	-	26	15	-	2.30
4-7 May	34	4	12	17	-	-		2.57	28	-	17	9	2	2.33
8-12May	13	-	9	4	-	-		(2.23)						

Table 3. Median profile scores of paired White-fronted Geese at Hvanneyri in spring, 1997 and 1998: a) with broods (hatched previous year); b) with accompanying adults (probably offspring from earlier years); c) unaccompanied by juveniles or adults (unacc.). n = sample size (same for both sexes); df = degrees of freedom. Chi-square from frequency distribution.

	1997 n	female	male	1998 n	female	male
a) + brood	32	4.06	3.00	78	3.69	2.78
b) + adults	46	4.42	3.16	54	3.77	2.97
c) unacc.	274	4.11	2.99	736	3.28	2.44
total	352	4.14	2.99	868	3.35	2.50
chi-square within year: df	4	8.38	3.65	6	23.82	35.84
P		>0.10	NS		<0.001	<0.001
chi-square between years + brood: df	2	9.56	3.51			
P		<0.01	NS			
+ adults: df	2	15.01	4.01			
P		<0.001	NS			
unacc.: df	3	158.22	45.11			
P		<0.001	<0.001			

Profiles and passage movements

Day-by-day changes in the numbers of geese using the Hvanneyri farm followed very similar patterns in 1997 and 1998 (Figure 6): a rapid early increase (16-20 April), a decline to about 25 April, a second, irregular, rise, then a rapid decline after 4 May. These changes suggest that as many as one-third of the arriving birds stayed for only a few days. Disappearances of marked individuals confirm this picture (unpublished data).

Geese passing through quickly might be expected to be fatter shortly after arrival than those staying longer. The early samples were small, because few geese were present. Only 6/380 females (1.6%) with scores of 5 were seen before 27 April, compared with 18/109 (16.5 %) on 27-28 April. There were similar disparities among paired males: no class 4 profile was seen until 24 April and only from 26 onwards did they become frequent (23/203 on 26-28, 11.3%). Thus geese leaving early are unlikely to have been fat.

From 28 April onwards about 60% of females had profile scores of 5 or 6, with remarkably little day-to-day variation. The proportion of males with profiles of 4 or more fluctuated around 30 %. The difference between these proportions and those at the time when the short-staying geese moved on suggests that profile increases in May may have been related more to reproductive development than to storing fat.

Social status and abdominal profiles

The median scores of pairs accompanied by adults or broods were higher than those of unaccompanied pairs (**Table 3**), especially in 1998, when the scores of all three categories were lower than in 1997. The disparities between the two years were less for accompanied than for unaccompanied pairs. Only 15/125 (12%) of juvenile geese (c.10 months old) had profiles as large as those of their female parents: 66 (52.8%) looked as fat as their male parents, though only one looked fatter. Many family groups of Greenland White-fronted Geese remain together, not only during the first year of life of the young but for several years afterwards (Warren *et al.* 1993). In 1997 and 1998, the profiles of some of these persistent family members, as well as those of their apparent parents, were noted. Here the results from both years are pooled, as the same tendencies were seen in each. Among birds in adult plumage closely attached to mature pairs, few (22/124, or 17.7%) seemed as fat as the females in those pairs, while 65 (52.4%) looked as fat as, and 12 (9.7%) fatter than, the parental males. Geese in adult plumage associated with pairs tended to have larger profiles than unattached adults.

Changes in the profiles of marked individuals

On most occasions when marked individuals were identified, their profiles could not be recorded because they were unsuitably positioned. Repeated records of individual profiles were obtained from only 18 adults and 8 juveniles in 1997 and 23 adults and 2 juveniles in 1998, by observers using the Owen scale.

Soon after first sighting in the period 18-23 April 1998 the profile scores of three adult females and four males decreased, two of the females by -1.0, which is unlikely to be due to observer inconsistency. Marked adults (> 1 year old) and juveniles (c.10 months old) both followed the tendency shown by large-scale scanning for profiles to increase from mid-April to early May. Yet the profiles of only two juveniles and five adults increased by as much as 3 half-points [e.g. from 1.5 to 3.0], while those of four adults and one juvenile, each seen on at least five different days during stays of at least 11-28 days, showed no net increase when last seen, though several of them had varied by 1-3 half-points during their stay. One very fat marked adult male (D4L, profile 3.5) was seen on 23 April 1997, an unusually early date for any goose to reach that level.

The proportion of marked juveniles reaching a score of 3.0 was significantly higher (6/10) than among marked adults of either sex (12/61, adjusted chi-square 5.41, $p < 0.025$).

The profiles of 21 collared individuals were recorded at least once in 1997 and 1998: 9 females, 11 males, plus one not sexed when marked but female by behaviour. The changes in their profiles during their stays paralleled the overall changes in median scores, with females having higher profile scores than males (Moods Median tests, $P < 0.05$). Both sexes showing the greatest gains in April and a steady state in May 1998, though with more variations in May 1997. The parents and three of the brood of four they had reared in 1996, which were marked at Hvanneyri in late April 1997, were seen again as a group on 21 April 1998 and remained at least until 2 May. The profile of the mature female increased by 1.0. The records of the others varied by no more than ± 0.5 during their stay.

Some profile scores of marked birds when last seen were as low as 1.5, especially among juveniles and unpaired adults (**Table 4**). This suggests that geese leaving for Greenland do not necessarily carry large reserves of abdominal fat.

Effects on profiles of feeding on different swards

In both 1997 and 1998, most of the profile samples from classified swards were from *Poa* fields. By grouping records into periods of several days, large enough samples from the other sward types were obtained to allow

Table 4. Abdominal profiles (0.5 scale) of individually recognised white-fronted geese when last seen at Hvanneyri in 1997 and 1998; data from both years pooled.

period	female profiles					male profiles				
	1.5	2.0	2.5	3.0	total	1.5	2.0	2.5	3.0	total
17-23 April	4	2	1	1	8	7	1	-	1	9
24 Apr - 1 May	5	5	3	-	13	4	4	3	2	13
2-7 May	2	8	8	7	25	5	5	4	9	23
total	11	15	12	8	46	16	10	7	12	45

some comparisons (**Table 5**), though *Deschampsia* was over- and *Poa* under-represented in 1997. In 1997 paired females on *Deschampsia* fields had much higher median scores than those on *Poa* fields in the period 24-29 April, but lower scores in 4-7 May (Moods Median tests, P < 0.05). In 1998, there were no differences in the median profiles of recently arrived geese seen on different swards (Moods Median tests, P > 0.05). Females on *Deschampsia* had much lower median scores in 24-29 April (i.e. had increased from 18-23 April far less than those on *Poa*) but by May were far below those on *Poa* (Moods Median tests, P < 0.05). Males showed no comparable disparities in either year (Moods Median tests, P > 0.05). Geese seen feeding on *Phleum* in the small areas in which it was dominant did not have exceptionally high median scores.

Discussion

The median late spring scores in Ireland were consistently higher in 1991 than in the other years of the study. The drop from scores in Ireland to those of recent arrivals in Iceland was much greater in 1991, but in 1990 and 1997, geese departed early from Wexford, so there were no records from this site in mid-April. However, data from a bird marked with a satellite transmitter showed that at least some of the geese departing from Wexford in early April 1997 staged in northern Ireland for at least 10 days before departure to Iceland (Glahder & Fox 1997). Hence, scores at the point of departure from Ireland were unavailable. The differences between 'departure' and 'arrival' scores in the other years presumably reflect variations in the energetic costs of the migratory flight.

The increases in profiles observed during the staging period were smaller and less consistent than expected. Certainly the rate of gain of fat deposits during spring staging is not as dramatic as those of Pink-footed Geese during an analogous spring staging period in northern Norway (Madsen 1995). As the second migratory journey, from Iceland to west Greenland, would be at least as far and as energetically costly as the flight from the wintering areas (involving a climb to over 2500m to surmount the icecap), it had seemed reasonable to suppose that the geese would leave Iceland carrying as much, or more, energy reserves as abdominal fat than when leaving Ireland or Scotland 3-5 weeks earlier. Although this appears to have been so in 1997, this is partly because of the early departure of

Table 5. Changes in median abdominal profiles of paired adult female and male White-fronted Geese feeding on swards dominated by *Deschampsia*, *Phleum* or *Poa* at Hvanneyri in 1997 and 1998.
n = no. pairs, F = female, M = male.

	Deschampsia			*Phleum*			*Poa*		
	n	F	M	n	F	M	n	F	M
1997									
24-29 Apr	46	3.98	2.96	-			16	3.26	2.80
30 Apr - 3 May	19	4.06	3.09	15	3.87		61	4.17	3.12
6-7 May	32	4.31	3.41	-			19	4.44	2.88
1998									
18-23 Apr	64	2.55	2.09	-			160	2.47	2.08
24-29 Apr	13	3.01	2.70	13	3.76	2.79	95	3.65	2.85
30 Apr - 3 May	-			16	3.93	2.96	60	3.82	2.93
4- 7 May	12	3.64	2.65	6	3.91	2.51	141	3.84	2.83

geese from Wexford to stage in northern Ireland before the flight to Iceland. Hence in all probability, geese apparently left Ireland in all four years of this study with greater fat reserves than when departing from Iceland. Certainly, there was little evidence from following marked individuals to suggest that individual performance (in terms of increases in profile score) showed any greater increase in fat deposits than suggested by the 'average' from scan samples presented here.

Inability to distinguish geese starting their second migratory flight from those perhaps dispersing to other sites in Iceland adds to the difficulty of using profile samples, coupled with daily counts, to follow changes in the state of individuals that might encourage, or delay, their departure. It seems likely that in most (if not in all) years geese arriving in west Greenland as early as 1 May would find sufficient snow-free vegetation to allow them to feed. Their normal procedure after arrival in Greenland is to remain near sea-level until snowmelt has progressed enough in their upland breeding areas to allow searching for nest sites to begin (Fox & Madsen 1981) even in years with late snow melt (Fox & Ridgill 1985).

It seems possible that in years with favourable weather systems over the north-east Atlantic Ocean, it would be feasible for geese leaving Ireland at the end of April with substantial energy reserves to fly directly to the southern tip of Greenland. The geese could then fly north along the west coast, a total distance of about 3300 km, without the need to climb over the icecap. There is no conclusive evidence that they do so, though this might come from future satellite tracking, which could also identify more about the performance of those geese that stop only briefly in Iceland.

How are the changes in profiles of the geese that remained in Iceland until well into May to be interpreted? Were these geese slower to reach migratory condition than the early-departing ones? Or were their decisions to remain late related to their unreadiness to breed, rather than lack of energy reserves for making a long flight? The levelling-off of the median scores of paired adults in early May suggests that accumulating fat for migration was no longer the highest priority, although it may just be that the fatter birds were leaving, balancing weight gains in other birds. The comparatively low scores of unpaired adults and juveniles confirm that fuel requirements alone do not oblige the geese to accumulate very large stores of fat. This is in contrast to the Brent Geese which also cross the Greenlandic icecap (Gudmundsson *et al.* 1995) which have much further to travel and will often find their breeding areas snow-covered in early June. Nevertheless, there is some evidence from this analysis that birds associating in larger groups (whether first spring or older offspring or their parents) may have a benefit in terms of nutrient acquisition, since such individuals showed higher than average profiles.

Whether variations in the beginning of grass growth in western lowland Iceland are linked to those in lowland west Greenland has yet to be studied. Nevertheless, given the advantages of earliest clutch initiation in most years, it is clearly of importance to potential breeding pairs to arrive in west Greenland as early as their fat stores will permit departure from Iceland. For other birds, depending on the relative state of food plant quality in Iceland and at the final staging areas in lowland west Greenland, in some years it could be profitable to move on early, while in others it might be better to remain in Iceland until at least the second week in May. The appropriate population response to such uncertainties would be relatively wide spread in the physiological states of individuals, as is evident in the range of profile scores in Iceland in spring. Madsen *et al.* (1997) found that Pink-footed Geese using spring staging areas in central and northern Norway showed differences between years and between sites in rates of increase of profiles and in departure scores. They also found that marked geese which were relatively fat when leaving north Norway to breed in Svalbard brought more young with them to Denmark in the following autumn.

Diet may have some influence on rate of fat accumulation, since there were striking differences between birds using the different grass swards. Clipping experiments at Hvanneyri have suggested that although *Deschampsia* has high biomass and protein content on arrival (compared with *Poa* for example), it is extremely slow growing, hence it is to be expected that early arrivals would benefit from feeding on this species but later on there is little food value in grazing the sward (unpublished data). In contrast, *Poa* grows relatively faster throughout the season and can be harvested almost continuously, although it is less nutritious (unpublished data). Though the nutritional value of *Phleum* is high (Fox 1993, Fox *et al.* 1998b), and the *Phleum* fields were less disturbed by road traffic than most other areas, geese using it did not have exceptionally high median scores. This may be because the sward is subject to sequential harvesting, and hence its profitability varies with the regrowth cycle following exploitation (Fox *et al.* 1998b).

Disturbance, too, could play a role. Nearly all geese seen in Myrar flew at the distant approach of a car, suggesting that they had been subjected to deliberate disturbance. That might account for the generally low profile scores in this area, and for the small increases in their profiles, compared with Hvanneyri, where the geese are tolerated on the fields and only subject to disturbance from regular farming activities. Madsen (1995) has demonstrated that such disturbance can inhibit accumulation of fat stores in Pink-footed Geese and this may have an effect on reproductive output of individual pairs.

How much is the change in profile linked to development of the sexual organs at this stage of the life cycle? Very little sexual activity by the White-fronted Geese was seen at Hvanneyri, although many small groups of geese flew, especially in mid-afternoon, to Vatnshamravatn, a lake on the east side of the farm, where they bathed, preened and slept briefly before returning to the fields. A few males started pre-copulatory displays, but rarely elicited positive responses from their mates, though sometimes provoking similar displays by nearby males, as seen among Pink-footed Geese by Boyd & Fox (1992). Less than ten hours were spent in afternoon watches at the lake in 1997 and 1998 and only three completed copulations, with full post-copulatory displays, were seen. As sexual activities occur on the water, the profiles of the geese are difficult to obtain. None of the females involved appeared to have the fully developed profiles characteristic of birds about to lay. Perhaps the sporadic activity in Iceland is due to a minority of males coming into reproductive condition early. Given the flight on to the ultimate Greenlandic breeding grounds and a delay of some 2-3 weeks between arrival and first egg dates, it seems likely that much of the major development of gonads (to the extent where it substantially affects profile scores) has yet to occur.

It would be useful to continue the assessment of profiles over several more years and to expand the geographical cover of staging sites. Enlarged samples should help to show whether profile sampling in Iceland could be used to predict subsequent breeding success in west Greenland. The findings reported here on the apparent enhancement of the condition of parents and full-grown offspring living in 'persistent families' also need to be verified and extended. Among White-fronted Geese breeding in the central Canadian Arctic, breeding pairs benefited from the defensive activities of their previous offspring, which enabled the adults to spend more time feeding just before nesting, while the yearlings were also able to feed more (Fox *et al.* 1995). Though the families broke up temporarily during the selection of nest sites and the laying period, the yearlings later gathered near the nests and effectively distracted nest predators. Thus continuing association between parents and their offspring seems to provide benefits to both generations.

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