Abdominal profiles of Icelandic Pink-footed Geese *Anser brachyrhynchus* in spring

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Pink-footed Geese in Scotland in mid-April had larger median abdominal profiles than those newly arrived at a lowland staging area in southwest Iceland in the second half of April. Their profiles returned to Scottish levels within about ten days of arrival and continued to increase until about 10 May, when many geese were leaving for their breeding places. Unpaired adults and those less than a year old had smaller profiles than paired adults, both before and after migrating. Paired females had larger profiles than their mates. In Iceland, females in isolated pairs or small groups tended to have larger profiles than those still in large flocks. The small numbers of paired females feeding on newly-tilled ground in Scotland and on rough pastures in Iceland tended to have smaller profiles than the majority feeding on improved grasslands in both countries. Increases in profiles in Iceland were directly associated with rising daily temperatures, which affected both the rate of snowmelt and the early growth of food plants. Annual breeding success (as measured by mean brood-size and the proportion of young found in Scotland in the autumn) was correlated significantly with differences in the median profiles of females and males in the previous early May. Although less informative about causation than detailed analyses of the body composition of dead geese, or repeated observations of changes in the profiles of individually identifiable live birds, scanning the profiles of relatively large numbers of unmarked geese yields results consistent with those from more intensive studies. This can help to decide which questions to ask about changes in the body condition of geese through the year, and their relationship to survival and breeding success.

Keywords: Pink-footed Goose, Spring Migration, Iceland, Body Condition, Abdominal Profiles

Analyses of the body composition of geese in spring have added greatly to our understanding of the physiological changes involved in preparing for northward migration, the intense social and sexual activities preceding egg-laying and the long incubation period (Ankney & MacInnes 1978, Raveling 1979, McLandress & Raveling 1981a,b, Gauthier *et al.* 1984a,b,c, Alisauskas & Ankney 1992). Although observations on the appearance of living geese cannot provide detailed physiological information, the "abdominal profile index" devised by Owen (1981) has proved useful as a means of comparing the abdominal fat reserves of different individuals at any one time and, when visibly-marked birds are available, of tracking changes in their state over time (Madsen 1985, 1995, Black, Deerenberg & Owen 1991). One purpose of this report is to show that, even when few marked geese are present, recording of relatively large numbers of profiles can be used to follow some changes in body condition that are associated with changes in overt behaviour, related to migration and preparations for breeding, and to suggest topics for more detailed investigation.

Over 200,000 Pink-footed Geese *Anser brachyrhynchus* now winter in Britain (Cranswick 1993), of which perhaps 10,000 breed in east Greenland (Boertmann 1994), the remainder in

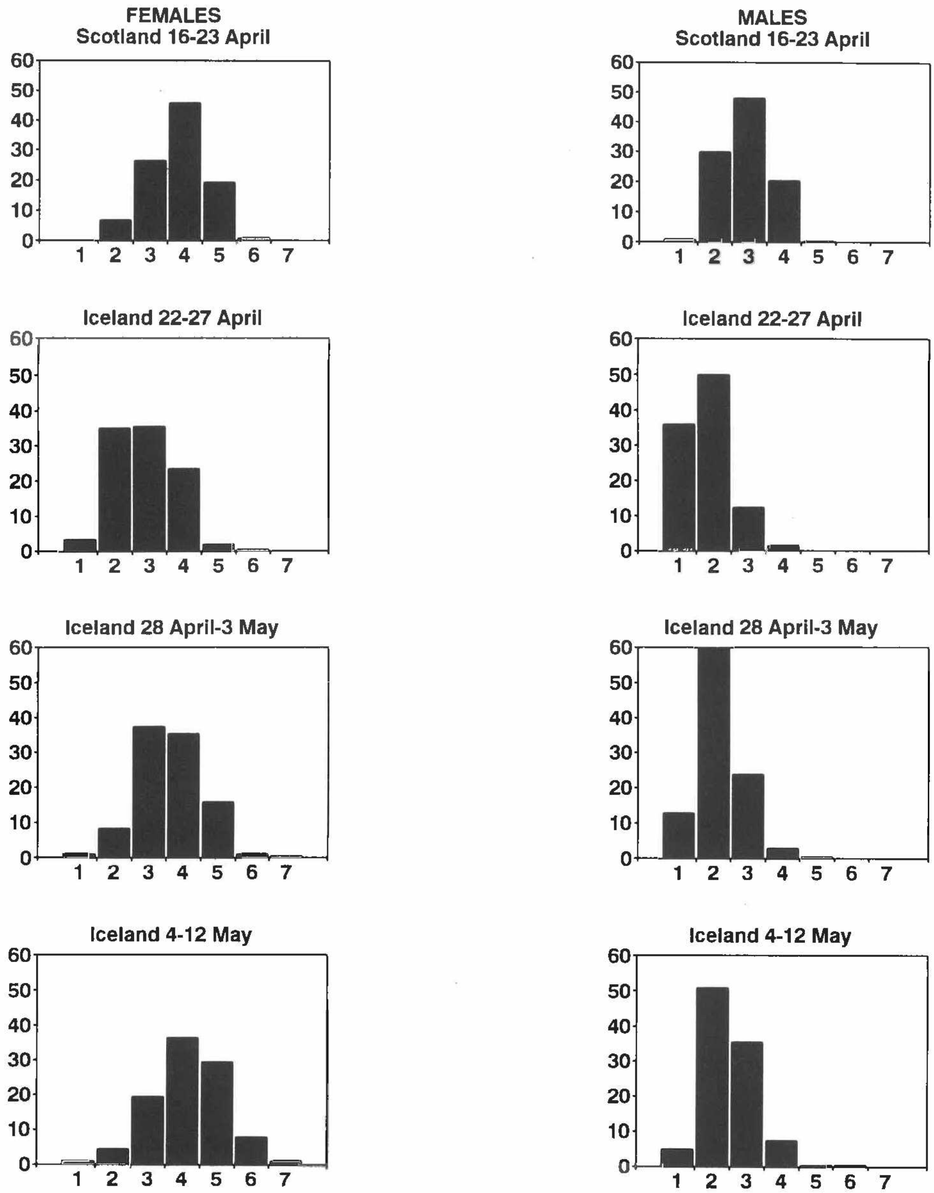


Figure 1. Frequency distributions of abdominal profile index (API) scores from Pink-footed Geese in Scotland and Iceland during spring 1989-1992 inclusive. Left hand histograms show females, right hand column males.

Iceland. These geese winter in several regions of Scotland and England. Most move to northeast Scotland in spring, before travelling 800-1,200 km in mid and late April to staging areas in the lowlands of Iceland, where they stay for two to five weeks before moving to nesting areas in the interior or travelling another 500-900 km to east Greenland. Most of the geese breeding in Greenland are believed to use staging areas in southeast Iceland (F. Gudmundsson, pers. comm.), while ringing recoveries show that the majority of those nesting in central Iceland assemble on agricultural land in the southwestern lowlands before moving to the interior (Fox, Boyd & Warren 1992, The Wildfowl & Wetlands Trust, unpub.). It is unusual for northern-nesting geese to have access to improved grasslands so close to their nesting areas, and it is only in the last fifty years that this source of forage has been available to them.

The Pink-footed Geese in Scotland in April have to accumulate sufficient energy reserves to journey safely to Iceland, while their reproductive systems are becoming active. This report describes their abdominal profiles before and after migrating, recording differences in the appearance of females and males, of paired and single adults and of geese not yet one year old. Changes after their arrival in Iceland are shown to be related to weather, as well as their internal state. Some implications of the observations are discussed.

Methods

Owen (1981) assigned the shape of the belly, which in females in spring reflects enlargement of the reproductive tract as well as the size of abdominal fat deposits, to one of four classes, a nearly-flat belly being scored as one and the distended belly of a female about to lay as four. Following Black, Deerenberg & Owen (1991), we used seven classes, introducing finer gradations within what is really a continuum. The scaling of abdominal profiles is not linear, and the relative uniformity in the condition of most individuals at any one time leads to a contracted frequency distribution, so that the mean and standard deviation do not define the distribution reliably. A weighted median is a more suitable single number to describe the state of a class (Owen & Black 1989); but for statistical comparisons it is preferable to use the entire frequency distributions, lumped when necessary to avoid small expected frequencies. Data from different sites or dates were tested for homogeneity (chi-square) and aggregated only when the differences were not statistically significant.

Geese were observed through telescopes at 50-400 m. Under favourable conditions (light overcast), active and dispersed geese less than a year old could be distinguished from older birds by remnants of juvenile plumage and lighter build (neck and upper body). The majority of older geese were in pairs, the males identified by larger size, higher carriage of the head and thicker neck. Attention was concentrated on mated pairs, as they provide the most useful information.

Most of the data were obtained in Iceland in 1989-1992, as a minor component of studies on the resources available to geese and how they were being used. Changes in numbers and distribution were monitored by frequent counts along a 40 km road circuit in Skeid, Árnessýsla (see **Figure 1** in Fox *et al.* 1992 for details), daytime activity budgets were compiled, and vegetation sampling showed when above-ground growth began and how much food of what quality was becoming available and being used (Fox *et al.* 1991, 1992, Fox 1993).

It would obviously be desirable to make observations in Scotland and Iceland in the same years, but the studies in Iceland were cut short for financial reasons in 1992. Observations in Scotland were limited to April 1993 and 1995.

Critics of the abdominal profile technique are sceptical both of what the observations can reveal about the birds' internal state and of the reliability and reproducibility of this 'subjective' rating procedure. Their concerns have best been addressed by Madsen (1995, and in prep.) who was able to make repeated observations on marked Pink-footed Geese wintering in Denmark, moving to north Norway in May and breeding in Svalbard. He found that, for both females and males, there was a significant linear relationship between weights at capture and the abdominal profiles scored immediately afterwards in the field. Tests in north Norway in May 1994 showed that Madsen (JM) and one of us (HB) assigned identical scores to most individuals, and differed by no more than one point in a few cases (Madsen & Boyd, in prep.) The scores used here were all made by the authors, nearly all those in Scotland by HB, those in Iceland in 1992 by ADF and the majority of the Icelandic records in earlier years by HB. There were few opportunities for us to score the same individuals at the same time and when we did our scores were not as consistent as those of JM and HB. In 19 cases where the same individuals were being observed, 12 ratings were the same, ADF>HB in two and ADF<HB in five, no differences being more than one point. Yet, for the analyses made here, it is the similarity of the patterns of frequency distributions obtained by the two observers on the same date that matters more than their scoring of the same individuals. **Table 1** compares our ratings on two occasions when we both inspected the same groups of geese, without attempting to look at the same individual at the same time. As with the known individuals, there was a tendency for HB to score higher than ADF, but the differences in the resulting distributions were not significant on either occasion. When looking at unmarked birds there is no opportunity to test the consistency of ratings by the same observer at different times. (As reported below, some of the distributions of scores by HB, looking at geese in the same fields on successive days in April 1995, were markedly different; but a biological explanation is suggested).

Profiles were recorded in Scotland during 19-23 April 1993 and 16-21 April 1995. The periods of observation in Iceland were: 25 April-9 May 1989; 12 April-6 May 1990; 16 April-3 May 1993 and 22 April-10 May 1992.

Verified weather records from Scotland are not yet available. The Icelandic meteorological data are from Vedráttan, the monthly and annual records published by Vedurstofa Íslands. Daily temperatures are not published for any station very close to the study area. Those for Reykjavík (64°09'N 22°00'W, 50 km to the west) are used. They closely resemble those from another lowland station, Kirkjubæjarklaustur (63°48'N 18°03'W) 150 km to the east. Our near-site observations with an unscreened thermometer did not show any major discrepancies. Because no profiles were recorded on a few days, it was necessary to lump the Icelandic data into five day periods before comparing profile frequencies with temperature changes.

Vedráttan also includes dates for the beginning of plant growth at some stations. Although the criteria used seem not to have been published, the continuity of observers at those stations should mean that their year-by-year recording was consistent. The May issue of Vedráttan nearly always includes dates of first spring sightings of many birds, including geese, which provide a rough index of annual variations of arrival times in Iceland, for comparison with changes in numbers of geese on the study area.

Results

Abdominal profiles in Scotland

The most comprehensive account of emigration of geese from Scotland to Iceland is that of Williamson (1968), based on both systematic observations in the Outer Hebrides and incidental records from mainland sites in the years 1953-1962. His chief conclusions were that: (1) goose emigration is stimulated by anticyclonic developments and the passage reaches a peak at such times; (2) cyclonic weather over the Atlantic may cause the geese to return to land,

Table 1. Abdominal profile scores assigned by ADF and HB on two occasions when both observers were rating pairs in the same small groups of Pink-footed Geese in Iceland. wm = weighted median (after Owen & Black 1989).

observer	pairs	female scores							male scores				
		1	2	3	4	5	6	wm	1	2	3	4	wm
21 April 1990													
HB	38	—	3	10	10	13	2	4.2	5	20	12	1	2.4
ADF		2	8	12	8	8	—	3.5	2	26	10	—	2.3
7 May 1989													
HB	22	—	—	1	10	7	4	5.0	—	4	13	5	3.1
ADF		—	—	—	6	9	7	5.1	—	8	10	4	2.6

Although in 3 of the 4 cases the wm of HB's scores is higher than that of ADF's, the differences between observers are not statistically significant (P>0.20).

Table 2. Frequency distributions of abdominal profiles of paired females and males, of single adults and of geese about 10 months old seen in Scotland in mid-April in 1993 and 1995. wm = weighted median.

	profile scores 1	2	3	4	5	6	7	*n*	wm
paired females									
1993	—	25	94	161	68	4	-	352	3.71
1995	—	51	162	153	56	10	1	433	3.05
paired males									
1993	4	105	169	73	1	—	—	352	2.79
1995	—	181	246	55	3	—	—	433	2.50
single adults									
1993 only	1	4	4	7	—	—	—	16	3.25
10 month-olds									
1993	3	60	43	4	—	—	—	110	2.73
1995	—	76	24	3	—	—	—	103	2.36

and inhibits migration in flocks about to put out to sea; (3) migration usually begins in the third week but has its peak in the fourth week of April; (4) emigration may be delayed in cold springs because of poor feeding conditions.

There have been large increases in goose numbers in the last 30 years, while great improvements in the condition of grass crops in the spring have increased the quantity and quality of food available to geese, in Iceland, as well as in Scotland. These changes make a thorough re-examination of spring emigration desirable. The contribution of observed variations in abdominal profiles is unlikely to be crucial, but they may help to establish the relative importance of feeding conditions and of the timing of favourable weather conditions in determining when emigration may be postponed or aborted, what proportion of the geese have begun sexual development before migrating (Boyd & Fox 1992) and whether the geese are likely to arrive in Iceland in good condition, so that their progress towards breeding will not be delayed.

In mid-April, paired adult females had larger median profiles than paired males, which were larger than young geese (**Table 2**). The samples of paired adults are disproportionately large, because they received most attention. The median profiles of all three classes were larger in 1993 than in 1995.

The profiles of geese in different districts varied (**Table 3**). The 'Easter Ross' sample was from Nigg Bay only in 1993, in 1995 it also included geese on

Table 3. Abdominal profiles of paired female and male Pink-footed Geese in different regions of Scotland in mid-April, 1993 and 1995. wm = weighted median.

	pairs	females 2	3	4	5	6	wm	males 1	2	3	4	5	wm
1993													
E.Ross	27	3	11	8	5	—	3.91	3	19	5	—	—	2.11
Buchan	127	14	36	56	20	1	3.48	1	50	55	21	—	2.45
Tayside	64	—	11	34	18	1	4.24	—	9	41	14	—	3.12
NORTH TOTALS	218	17	58	98	43	2	3.69	4	78	101	35	—	2.53
Lothian	45	—	3	22	18	2	4.77	—	2	20	22	1	3.48
Solway	89	8	33	41	7	—	3.17	—	25	48	16	—	2.81
SOUTH TOTALS	134	8	36	63	25	2	3.73	—	27	68	38	1	3.18
1995													
E.Ross	186	48	78	53	7	—	3.15	—	103	79	4	—	2.81
Buchan	237	3	79	96	48	11*	3.76	—	54	136	44	3	2.95
Tayside	10	—	5	4	1	—	4.00	—	4	6	—	—	2.33
NORTH TOTALS	433	51	162	153	56	11	3.55	—	161	221	48	3	2.50

* includes one of class 7

the Black Isle. There were no significant differences in the relative frequencies of profiles of paired females between sites or between years but the distribution of paired male profiles differed greatly between years, with a mode of three in 1993 (70% of the sample) and two (65%) in 1995.

In 1993, paired females tended to have larger profiles in Ross than in Buchan. The reverse was true in 1995. In both years 'Buchan' included samples from Lossiemouth, the Loch of Strathbeg and Meikle Loch. Within Buchan, proportionately few paired females using the Meikle Loch had profiles larger than four in either year, while larger females were plentiful near the Loch of Strathbeg in both years and at Lossiemouth in 1995.

'Tayside' included Strathallan and Strathearn, with a few from Kinross in 1993. Few Pink-footed Geese remained in Perthshire or further south by 16 April 1995, so that it was not possible to obtain useful numbers of profiles from there, or any from the Lothians and Solway. In 1993 these southern samples departed most from the total distribution.

In 1995, profiles were recorded for geese using a single farm near the Loch of Strathbeg on three successive days (17-19 April). The numbers of geese present were between 2,000 and 3,000. Both in the early morning (18th, 19th) and in the early afternoon (17th), a large proportion of them were sitting down. Whether the few that were feeding were representative of the entire group is not known, nor whether the same individuals came each day. Although the relative frequencies of male profiles did not vary significantly, there were more female profiles of five or six on 18th (19 of 27, mode five) than on 17th (11/27, mode four) and 19th (8/39, mode two). Although it would be unwise to speculate on the interpretation of these differences, they suggest that sustained watching at a single site may prove useful, especially if combined with daily censuses of the geese using the relevant roost. Another observation that needs to be followed up is that the minority (94, or 22%) of paired females feeding on newly-tilled fields (on which no plants could be seen) included 75 (nearly 80%) in classes two and three and only one class five. The corresponding proportions in those feeding on grass were 41% [two plus three] and 19% of five plus six. It seems more likely that these 'thin' geese were searching for some element in the diet not found in 'improved' grass, than they were unable to compete on grass. There was no comparable disparity in the profiles of paired males.

That the Pink-footed Geese seen in northern Scotland tended to have smaller profiles than those seen on corresponding dates in 1993, while fewer geese were to be found in the south, suggests that emigration was further advanced in 1995. The working supposition is that geese will leave, weather permitting, when they have accumulated sufficient reserves of energy to enable them to reach southern Iceland without difficulty. Williamson's (1968) findings that geese encountering cyclonic conditions may turn back to Scotland, to await more suitable conditions, suggests that the "prudent Pinkfoot" should invest in ample reserves, especially as conditions in Iceland in late April are often unhelpful for rapid recovery of depleted reserves. Young geese, and unpaired adults, can apparently travel successfully with smaller reserves than paired adults. This suggests that paired females with profiles of five or six (20% of the sample in 1993 and 15% in 1995) were carrying more than they needed for the journey alone. But very few (perhaps no more than 1% in 1993 and 2.5% in 1995) had profiles of six (or seven), which become frequent in Iceland in the second week of May (see below).

Abdominal profiles in Iceland

Among the paired geese seen in Scotland in 1993 and 1995, 40% of females were in class four and nearly 50% of males in class three (**Table 3**). This disparity of one class between the modes of males and females persisted in Iceland. The contrast between the sexes was especially marked at the extremes. Very few females were classed as one, and very few males as five (although in the second week of May more than a third of the females had profiles of five

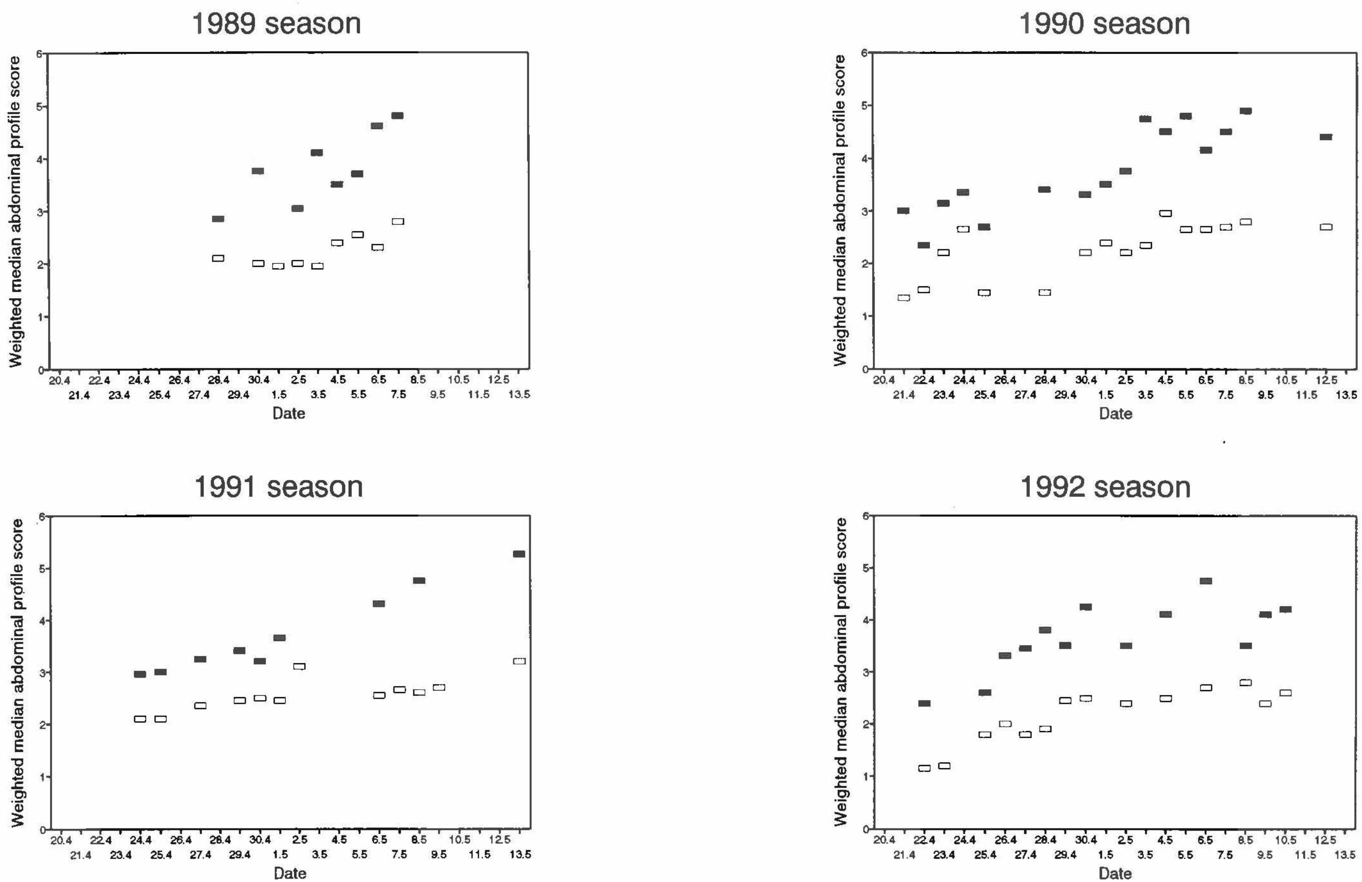


Figure 2. Daily weighted median abdominal profile scores for males (open symbols) and female Pink-footed Geese (closed symbols) in each of the springs of 1989 to 1992.

or more). **Figure 1** summarises changes in class frequencies in Iceland during late April and early May (pooled data from four years).

There are large differences between the summed profiles on 16-23 April in Scotland and 22-27 April in Iceland. The high proportion of class one male profiles seen soon after arrival in Iceland suggests that the flight from Scotland to Iceland uses up most of the abdominal fat deposits. Presumably the amount of fat consumed by females during migration is much the same, though its disappearance is partially offset by the enlargement of the reproductive tract, which begins in Scotland, but accelerates after arrival in Iceland.

Figure 2, using weighted medians,

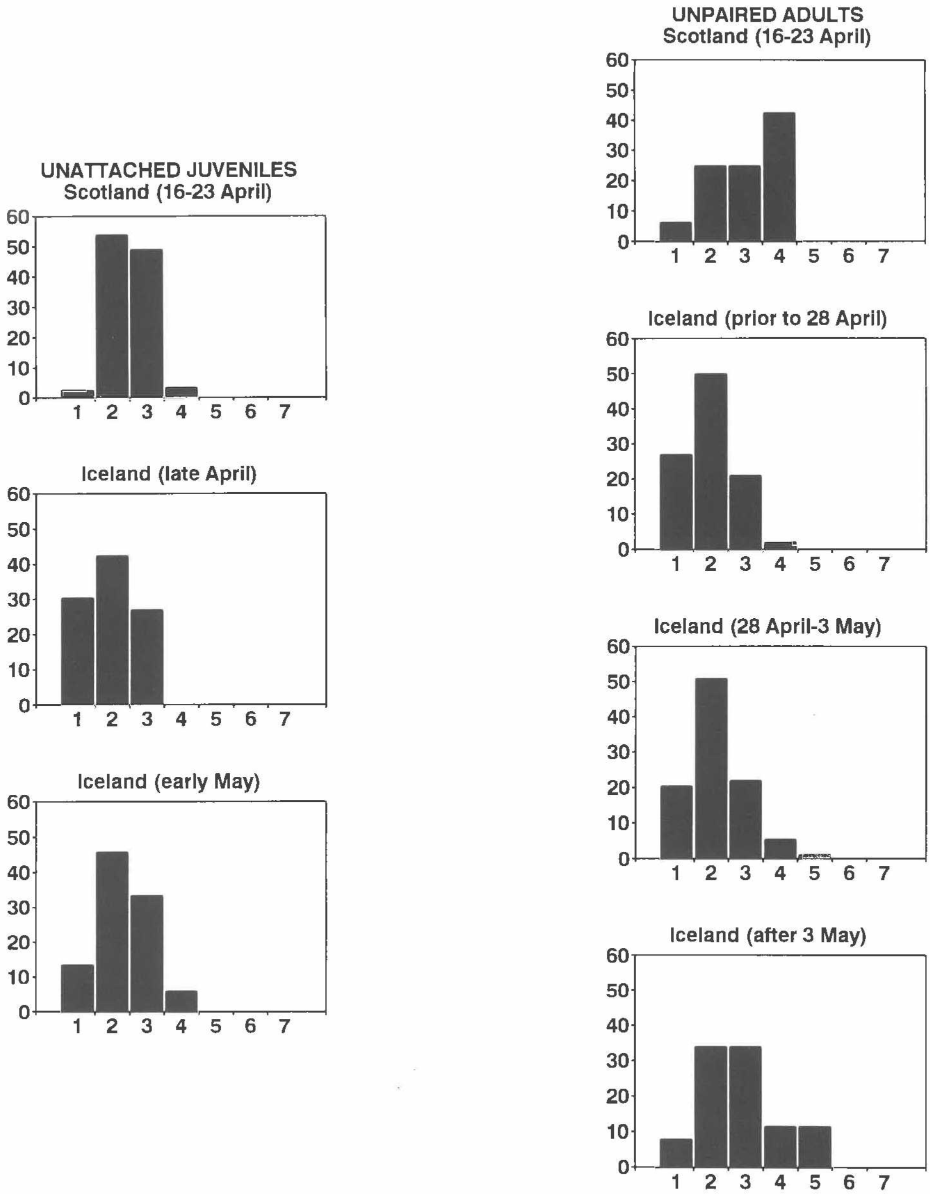


Figure 3. Frequency distributions of abdominal profile index (API) scores from Pink-footed Geese in Scotland and Iceland during spring 1989-1992 inclusive. Left hand histograms show unattached juveniles, right hand column unpaired adults.

Table 4. Reported dates for start of spring plant growth at five stations in Árnessýsla, 1989-1992.

	location	height a.s.l.(m)	1989	1990	1991	1992	mean 1981-92
Önnupartur 63°44'N 20°37'W	coast	10	3/5	5/5	28/5	11/4	3/5
Reykir 64°00'N 21°11'W	lowlands	51	4/5	8/5	27/4	24/4	2/5
Irafoss 64°06'N 21°01'W	lowlands	66	23/5	21/5	14/5	24/5	13/5
Sámsstadir 63°44'N 20°07'W	lowlands	90	23/5	23/5	4/5	18/5	15/5
Jadar 64°17'N 20°10'W	uplands	135	—	27/5	2/5	14/5	16/5

gives a more detailed picture of the daily increases in profiles from arrival in Iceland to the departure for nesting places 5-15 May. Female median profiles were higher throughout, and increased more rapidly and more steadily than those of males, which showed little increase after 4 May. As we were unable to search the central highlands each year, we do not know when pairs ready to breed moved away from the lowlands. An aerial survey of the Thjórsá valley and Thjórsárver (65°40'N, 18°40'W) on 9 May 1989 found the interior almost wholly covered in snow, with very few geese, none nesting.

In 1990, during a period of sub-zero daily mean temperatures (which are quite frequent in the lowlands in late April), male profiles remained low for several days after 25 April, while the females showed a briefer check. A common pattern of increasing profiles was found in all four years, seeming to end earlier for males than for females.

The profiles of single adults and of geese less than a year old, grouped by dates, are shown in **Figure 3**. Because the numbers are small, actual frequencies, rather than percentages, are given. Singles in Scotland tended to have higher profiles than those in Iceland later in April, although by May there were several in class five, not seen in Scotland.

Among yearling geese, most still with their parents, very few of those seen in Scotland in mid-April were in class one, noted frequently in Iceland later in April. No class five yearlings were noted. Young geese not with their parents had lower profiles than those in families, both before and after migrating, (significant only at the level of P=0.10).

Arrival and build-up of numbers in south Iceland

Most of the earliest Pink-footed Goose records have been reported from Kvisker (63°59'N 16°28'W), 130 km southeast of Thjórsárver and 200 km

Table 5. Different measures of snow cover phenology in Árnessýsla, 1989-1992. Data from individual stations are pooled by region, namely coast (5-10 m a.s.l., n=4), lowlands (15-90 m, n=5), uplands (101-135 m, n=4), Hveravellir (at 641m a.s.l.).

	1989	1990	1991	1992
days in Apr/May with total snow cover				
coast	10	15	4	4
lowlands	6	12	3	4
uplands	8	19	2	3
Hveravellir	31	42	46	55
last date of total snow cover				
coast	14/5	27/4	15/4	5/5
lowlands	14/5	27/4	14/4	7/5
uplands	14/5	5/5	18/4	6/5
Hveravellir	4/6	26/6	19/5	25/5
date of end of snow cover				
coast	16/5	8/5	20/4	3/5
lowlands	16/5	11/5	6/5	8/5
uplands	20/5	10/5	14/5	9/5
Hveravellir	30/6	27/6	10/6	29/6

Table 6. Comparisons of distributions of early abdominal profile frequencies from the period 20-25 April, 1990-1992.

	paired females				paired males		
	1,2	3	4-6	total	1	2	3,4
1990	52	33	29	114	46	43	25
1991	21	35	20	76	10	50	16
1992	43	29	6	78	53	24	1
total	116	97	55	268	109	117	42

4 d.f. chi-square: females 19.55, $P < 0.001$ males 64.28 $P < 0.001$

east of the study area, where since 1950 the mean date of first sighting has been 19 April ± 4 days (n=21), although Björnsson (1976) noted "They rarely arrive before April 20 and mostly from April 25-30." In 1989 the first at Kvisker were on 16th; in 1990 – 22nd; in 1992 – 21st. In 1991, the first reported sighting was on 15 April, at Bru (65°06'N 15°32'W), in the northeastern interior; the first geese at Kvisker were presumably later.

Our observations in 1989 did not begin until 25 April, well after the first sighting at Kvisker. In the other years geese arrived in the study area very soon after the first Kvisker sightings. First Pinkfeet were seen on the Skeid circuit on 21 April 1990, 21 April 1991 and 24 April 1992.

Local phenology

Table 4 records the start of plant growth at five stations around the Skeid study area, as reported in Vedráttan. Growth initiation is progressively delayed with increasing altitude, although in 1991 growth began very late even on the coast (as was also reported from Vik i Myrdal 63°25'N 19°01'W, 100 km further east).

Table 5 summarises information on the timing of snowmelt in Árnessýsla, including the highland station at Hveravellir (64°52'N 19°34'W, 641 m a.s.l.), where the summer climate is similar to that in Thjórsárver (Gardarsson 1976). Except at Hveravellir, total snow cover was infrequent in May, and in 1991 and 1992 also in April. On average, snow cover near the coast ended a week earlier than in the interior lowlands and seven weeks earlier than at Hveravellir. The interval between the date of last total snow cover and that of its final disappearance increased with altitude (coast four days; lowlands and uplands ten days; Hveravellir 21 days).

Fox *et al.* (1991) found that the geese were able to start feeding as soon as small areas became snow-free, exploiting the receding edges of snow-patches, where the grass was greener, as a result of its protection under the snow from the effects of frost. Thus the relationships of goose feeding to snowmelt and the start of plant growth are interwoven.

Ranking years according to start of plant growth and time of last total snow cover suggest that 1992 was the 'earliest' year, followed by 1991 and 1989, with 1990 the 'latest'. Yet, perhaps because of a prolonged cold spell in the first half of May, 1992 proved to be the poorest breeding year for Pinkfeet (see below).

Profiles soon after arrival

Observations in 1989 did not begin until 25 April, when the geese were well established. In 1990-1992, the profiles of geese seen from 20-25 April showed marked differences in class frequencies (**Table 6**) among paired males and females. The relative scarcity in 1991 of class one and two females, and class one males, suggests that they had arrived in better condition, or earlier, than in the other years. In 1992 thin birds were relatively common and classes four to six females and three to four males very scarce, suggesting that they had either been in poorer condition when leaving Scotland, had a difficult migratory flight, arrived late, or had been affected by a combination of these.

Profiles on unimproved land in Iceland

The great majority of geese fed on farmed land, mostly on improved

Table 7. Comparisons of distributions of abdominal profile frequencies from pairs feeding on rough grasslands and on improved farmland, 3-7 May, 1989 and 1990.

	paired females				paired males	
	1-3	4	5-7	total	1,2	3-6
rough grass	28	15	16	59	38	21
improved land	184	297	292	773	447	326
total	212	312	308	832	485	347

chi-square: females (2 d.f.) 16.19, $P < 0.001$; males (1 d.f.) 0.98, NS

grasslands, with a preference for recently reseeded grass, but also on unploughed stubble and potato fields, in those districts where they occurred, chiefly near the coast (Fox *et al.* 1992, Fox 1993). Some fed on rough grasslands, both wet and dry. Because few did so, it was hard to obtain adequate samples. Yet, from 3-7 May in 1989 and 1990, when 7% of the profiles recorded (**Table 7**) were of pairs feeding on rough grass, those females tended to be thinner than the females on improved grass. There was no difference between male profiles.

Profiles and daily mean temperatures

The changes in the median profiles of paired females and males during late April and early May were highly correlated with daily mean temperatures at Reykjavík in all four years (**Table 8**). This simple model explained more of the variance than others that were tried: cumulative °C/days; cumulative °C days >0°C and a mix of date and all these parameters. Adding (local) precipitation to the models did not explain additional variance. The effects of rain or late snowfalls are likely to be very short-term, and amounts often vary greatly across short distances in southwest Iceland.

Monthly mean temperatures at Reykjavík in 1961-1990 were 2.9°C in April and 6.3°C in May. Variations about these levels should cause no direct problems for geese. However, the upward trend in daily temperature seems to act as an effective proxy for the many environmental variations that determine how efficiently geese can feed in southwest Iceland in the spring. When the deviations from the upward trends in median profiles and in temperature were compared they showed no relationship, but there is no reason to expect a linear response in the abdominal profiles to a change of a few degrees, although the geese often shift feeding places when snow or frost alter access to high-quality food plants.

In 1989-1991 the seasonal rise of daily temperatures was checked for a few days in late April. In 1992 no check took place until well into May. The increase in median profiles was smoothest in 1992. Perhaps by early May ground temperatures are high enough to enable plants to keep on growing, despite air frosts.

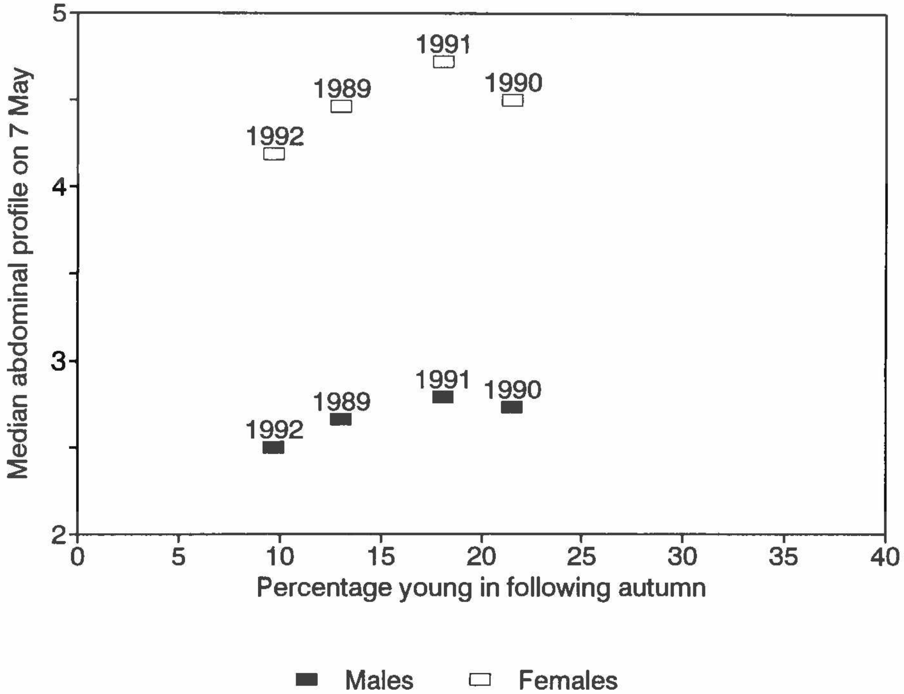
In 1989, the first half of April was unusually cold, but the daytime temperatures rose more rapidly in the second half of the month than in the later years. The geese put on weight faster in 1989, despite an apparent lack of grass growth (Fox *et al.* 1991). This suggests that weather conditions in Iceland may be more important than those in Scotland in enabling these geese to reach breeding condition early.

Profiles and breeding success

We know of no records of the dates on

Table 8. Correlation coefficients of median paired female and male Pink-footed Geese scored in southern Iceland with daily temperatures in Reykjavík in late April/early May of the four years of study.

	Sex	$\%r^2$	F-ratio	P
1989	FEMALE	70.3	16.6	0.005
	MALE	61.8	11.3	0.012
1990	FEMALE	75.8	43.8	<0.001
	MALE	57.0	18.6	<0.001
1991	FEMALE	95.7	154.12	<0.001
	MALE	51.5	10.6	0.009
1992	FEMALE	53.3	12.56	0.005
	MALE	76.3	38.5	<0.001



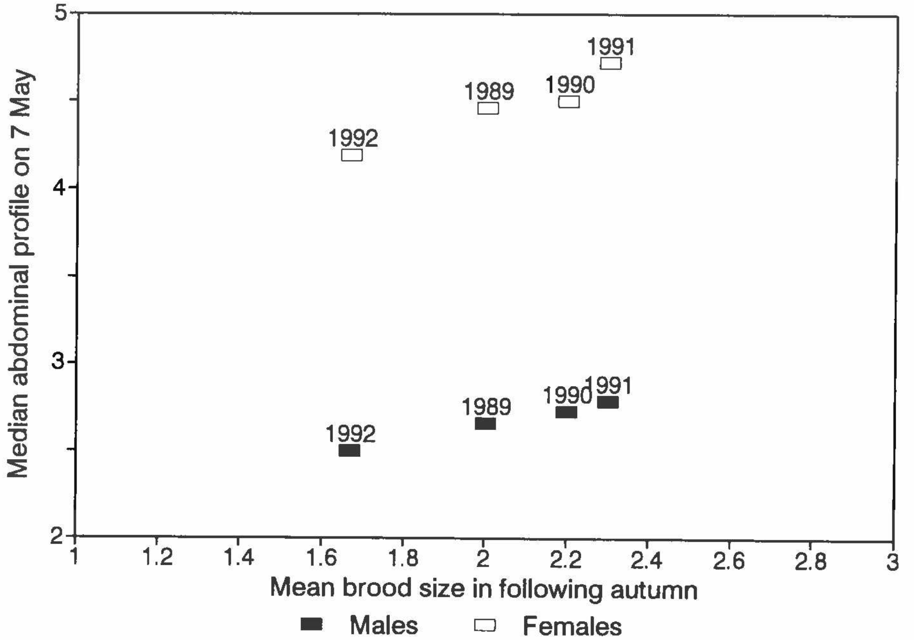


Figure 4. Graphs of (upper) percentage young and (lower) brood size amongst sampled populations of Pink-footed Geese in Britain in autumn and female API score on the preceding 7 May. Correlation coefficients for the relationships were: API v. percentage young females r = 0.99***, males r = 0.85** ; API v. brood size: females r = 0.86**, males r = 0.99***.

which Pink-footed Geese began to lay in Iceland in 1989-1992. Gardarsson (1976) found that in 1971 and 1972 the mean hatching date in the Thjórsárver colony was 19 June, from which, assuming a mean clutch size of 4.6, he inferred a mean laying date of 21 May, though he noted that some females had laid by 16 May. Scott, Fisher & Gudmundsson (1953) estimated from hatching dates that in 1951 the first eggs must have been laid about 12 May, with the peak date for complete clutches (mean 4.5) about 25 May. In 1953, peak hatching (and therefore clutch completion) seems to have been a little later (Scott, Boyd & Sladen 1955). As noted earlier, no pairs seen during the aerial inspection of Pjórsárver on 9 May 1989 were at nests.

The median profile score on 7 May (five to seven days before the expected beginning of egg-laying), being the latest data available in all four years, can be used as an index of the breeding condition of female Pink-footed Geese each year. With no direct records of nesting effort, brood-sizes at hatching or fledging in 1989-1992, we are obliged to use information obtained in autumn in Britain, soon after the arrival of migrants from Iceland. Assuming that losses of young geese on migration were small, or constant, in those years (Patterson & Giroux 1990), the percentage of young geese in flocks and the mean size of broods seen in Britain provide annual indices of breeding success. In years when pairs were in relatively poor condition in early May, their subsequent breeding success was less than in years when their May reserves were larger (**Figure 4**). The correlation coefficients were larger for males than for females.

Discussion

The greater increases in Iceland in the profiles of paired females, compared with those of their mates, reflect both differences in internal state and in behaviour. The female reproductive apparatus enlarges far more than that of males, and females are enabled to feed far more assiduously, because paired males spend much of their time alert, rather than feeding, in order to protect their mates from predators and, more importantly and much more often, from the attentions of other males.

The comparative flattening of the profile growth curve of males in early May could also result from their having acquired sufficient reserves to carry them through the laying period, when they have no eggs to lay, but may need to be very active in defending their mates. Once incubation is under way, males are able to feed over much of the day, while females can only do so in short breaks away from the nest.

Despite the small sample sizes and data from only four years, the profile frequencies suggest links between the spring profiles of both females and males and subsequent measures of breeding success. These relationships may be improved by data collection in more extreme years, since the springs of 1989-1992 were neither especially mild nor severe, and the breeding success and brood size among Pinkfeet returning to Britain in those autumns varied little compared with longer runs of data.

The comparatively thin state of unpaired adults (presumably mostly two-year-olds and other pre-breeders) and yearlings may again reflect a lack of need to develop reserves, as they will be free to continue feeding throughout the summer. Among Pink-footed Geese caught in Britain in October and November, geese in their second autumn of life still tended to be smaller, and weigh less, than mature adults (Beer & Boyd 1962).

The results reported here raise more questions than they answer. Much more needs to be learned about variations in the condition of geese in Scotland prior to migration. There have been major changes in spring distribution in recent years (Thom 1986), with increasingly large concentrations in the northeast (Buckland, Bell & Picozzi 1990). The dependence of geese on the "spring bite" has long been appreciated (Brotherston 1964, Newton, Thom & Brotherston 1973). There is also need for a fresh look at what agronomists, farmers and changes in climate have done to alter the quality, timing of growth and geographical distribution of high-protein grasses in April, which until half a century ago was a period of dearth in Scotland (Parry 1978, 1980).

In Iceland, more needs to be learned about the reasons for and the effects of, the recent expansion of breeding Pink-footed Geese from their highland strongholds into the lowlands, where they seem likely to come into increasing competition with Greylag Geese, the traditional occupants of the lowlands, which are also much more numerous than formerly. Whether the minority of geese feeding on unimproved pasture in the lowlands were doing so as a result of behavioural exclusion or disturbance from elsewhere is not known. That they had lower API scores than those on adjacent reseeded grassland may have considerable historical importance. Artificially managed grasslands have only existed in the area for the last 30-40 years. The poorer condition of birds on rough grassland suggests that, prior to agricultural improvement, Pink-footed Geese would have either (i) commenced breeding in poorer condition at a similar time, or (ii) delayed nesting to give sufficient time to accumulate equivalent reserves for breeding. Both of these scenarios would likely have reduced the reproductive potential of mature pairs, compared with conditions they experience today. This is a time of rapid agricultural and landscape change in Iceland, where support programmes for farmers have been greatly reduced since 1990 (OECD 1993a,b). Whether the geese will gain or lose from what is to come is far from clear; but they must continue to be monitored and studied, both in Iceland and in Britain, if they need help to continue to thrive, as they have done in the second half of the twentieth century.

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