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A combination of ringing recoveries, resightings of individually marked birds and regularly counted census routes suggest that Greenland White-fronted Geese stage in Iceland from c.10 April until c.12 May in spring and c.30 August until c.31 October in autumn. Observations confirm that there are two main areas used by the population, the southern lowlands (Árnessýsla, Rangárvallassýsla and Vestur-Skaftafellssýsla) and the western lowlands (Kjósarsýsla, Borgarfjarðarsýsla, Mýrarsýsla and Snæfellsness- og Hnappadalssýsla) which are exploited in both spring and autumn. Spring migration phenology appears to differ between areas, with earlier arrivals in the southern lowlands where numbers beaked during 24-26 April in 1990-1992, compared to a rapid build up in western staging areas to peak numbers during 18-22 April in 1997-1999, where substantial numbers of birds remained well into May each year. These differences most likely relate to the timing of migration in the years concerned, but could also reflect different migration strategies of birds using the two areas (records of individuals using both staging areas are rare). At the most important staging site in the western lowlands, Hvanneyri, up to a maximum of 1500 birds were counted. Based on observations of individually marked birds at Hvanneyri, more than half of the geese remained for less than a week, mostly early on in migration, whilst more than a third stayed for almost the entire staging period (c. 24 days). More detailed information relating to the behaviour of individuals is required to fully understand the importance of the staging periods in Iceland to this goose population.

Keywords: Greenland White-fronted Geese, Iceland, migration, stopover, turnover.

he discrete population of Whitefronted Geese that breeds in west Greenland and winters in Ireland and Britain passes through Iceland on migration in spring and autumn (Fox et al. 1999). In this respect, the Greenland White-front is different from most other arctic goose populations in that it must make two migration flights of more than 1000 km across two areas of open sea to arrive at its breeding areas. The Greenland Barnacle Goose Branta leucopsis and the Greenland-breeding element of the Pinkfooted Goose Anser brachyrhynchus population that winters in Britain show a similar two-stage migration pattern. However, both breed on the east coast of Greenland (Mitchell et al. 1999; Ogilvie et al. 1999) and therefore do not traverse the

large Greenland Ice Cap to arrive at breeding areas as do the Greenland White-fronts (Alerstam et al. 1986; Glahder et al. 1998). Only the Light-bellied Brent Goose which breeds in arctic Canada and winters in Ireland takes the same route in spring (Merne et al. 1999).

Since the first major account of staging White-fronts in west Greenland, we now know that a substantial proportion (if not all) of the population stages in Iceland in spring (Francis & Fox 1987). Using field scores of abdominal profiles, it would appear that the coastal lowlands of southwest and western Iceland provide important feeding opportunities after the 1000-1500 km flight from wintering areas (Boyd et al. 1999). Since the onwards flight to ultimate breeding areas involves a

further flight of at least 1400 km, involving the crossing of the extensive and high (>2500 m) inland ice cap, accumulation of body stores in Iceland is likely to be critical to their ability to complete this journey. In the same way, most (if not all) of the population is thought to stage in Iceland in autumn, en route along the same migration pathway back to the winter quarters. The species is legal quarry there in autumn when up to 3,500 individuals are shot annually (Sigfusson 1996; Fox et al. 1999).

In considering the ecological significance (and hence the importance in nature conservation terms) of staging in Iceland, it is important to have some basic understanding of the timing and nature of migration episodes and geographical distribution of areas used. In this paper, we use existing information from ringing recoveries and the resightings of individually marked Greenland Whitefronted Geese to assess the timing and nature of spring and autumn staging by the population in Iceland. We combine these findings with data from various sources to describe their geographical distribution and speculate upon their migration strategies.

Methods

The analysis presented here is based upon numbers of Greenland White-fronted Geese captured for the purposes of ringing from a variety of sources since 1946. The earliest metal ringing started after the Second World War, and some 1319 were marked with metal rings on the breeding grounds in Greenland during the period 1946-1974 under the scheme organised by the late Finn Salomonsen from the Zoological Museum in Copenhagen (for see details in Kampp et

al. 1988). Of these, 18 geese had been reported (all shot) from Iceland.

Since 1983, 1446 Greenland Whitefronted Geese have been captured in Ireland and Britain and fitted with engraved plastic collars and/or leg rings as well as standard British Trust for Ornithology metal leg rings. Of these, 1328 have been marked at Wexford Slobs in SE Ireland by the National Parks and Wildlife Service (56 of these bearing leg rings only) and a further 67 collared at other sites in Ireland. In addition, 37 geese have been caught on Islay in Scotland (14 with plastic leg rings, the remainder with collars as well), one fitted with a plastic leg ring in Lancashire and seven collared in Iceland. A further 348 geese have been captured in Greenland during moult since 1979, all bearing metal Copenhagen Museum rings, 192 bear leg rings only and the remainder were fitted with collars and leg rings. These individually marked geese have generated over 46,000 resightings from over 200 observers up until the end of May 1999. The observations of these individually marked birds from Iceland consist of 1321 observations of 329 different individuals on 133 dates at 60 different sites (we here define a "site" as a separate farm or other land holding as on the 1:100,000 scale Landmælingar Íslands maps of Iceland). In addition, 174 of these geese have been recovered and reported as dead from Iceland. These were predominantly shot birds, excepting three found sick and destroyed (probably shot), one instance of the ring only being found and two geese found long dead. These recoveries came from 108 different sites; most sites have supported one (73 sites) of two (23) recoveries, but four sites have produced larger numbers of recoveries, namely Bóndhóll (Mýrarssýsla 64°31'N 22°06'W)

and Pykkvibær (Rangárvallassýsla 63°45'N 20°37'W) with seven recoveries each, and Leirulækjarsel (Mýrarssýsla 64°35'N 21°50'W) and Kolvi∂arnes (Snæfellsnessog Hnappadalssýsla, 64°48'N 22°27'W) with eight recoveries each.

The resighting effort has not been constant, and the various biases in observer effort in time and space must be considered in using these data. In 1986, two expeditions (in spring and autumn) travelled to Iceland to survey the western and south-western staging areas described by Francis & Fox (1987). At that time, all numbers were counted and the presence of individually marked birds recorded. Since 1989, JÓH and ÓE (aided by other observers) have visited the Andakílsá area of Borgarfjördur in western Iceland on I May in every spring to count numbers present within a specified count area. This centred on the fields and marshes of the Hvanneyri Agricultural College, but extended to the flood meadows of the Andakílsá and Hvítá rivers to the north and south of this important staging area. In recent years, resightings of individually marked birds have been reported by many Icelandic observers, most notably by Gu∂ni Sigvaldsson Þykkvibær, Rangárvallassýsla, and maintained in a central database. During the springs of 1989-1992 inclusive, the Wildfowl & Wetlands Trust undertook expeditions to the southern lowlands of Iceland to study the pre-nesting ecology of Pink-footed Geese there (eg Fox et al. 1991, 1992). In the course of these and other investigations, reports of individually marked Greenland White-fronted Geese were gathered by teams active in the field and numbers of birds were counted along defined census routes driven on a regular basis to monitor daily changes in Pinkfooted Geese and Greylag Geese Anser anser numbers. In particular, we counted

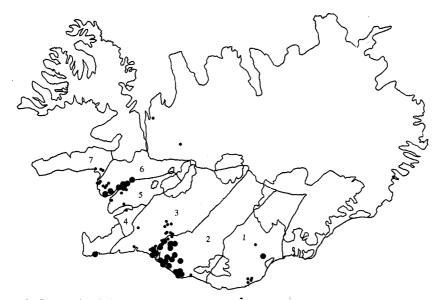


Figure I. Geographical distribution of ringing recoveries of all Greenland White-fronted Geese, marked in Ireland and Greenland and recovered and reported from Iceland up until I June 1999. Numbers indicate counties as follows: I - Vestur-Skaftafellssýsla, 2 − Rangárvallassýsla, 3 - Árnessýsla, 4 - Kjósarsýsla, 5 - Borgarfjar∂arsysla, 6 - Mýrarsýsla and 7 - Snæfellsness- og Hnappadalssýsla.

Greenland White-fronted Geese along two transects in the southern lowlands. Firstly, a 40 km road transect in Skei∂, Árnessýsla (see Figure I in Fox et al. 1992 for precise location) driven at approximately the same time on as many dates as feasible during 12 April-6 May 1990, 16 April-3 May 1991 and 22 April-10 May 1992. Secondly, we counted all visible geese along the road from Fljótshólar (63°47'N 20°48'W) to Villingaholt (63°53'N 20°45'W) in Flói, Árnessýsla during 12 April-6 May 1990.

During the springs of 1997-1999, observers (including most of the authors) were based at the Hvanneyri Agricultural College to undertake ecological studies of the staging geese. Observers were present during 17 April-9 May 1997, 18 April-7 May 1998 and 15 April-10 May 1999. On the college farm, counts of all fields and the

adjacent intertidal marshes (dominated by Carex lyngbyei vegetation) were carried out on a daily basis, with a minimum of three counts carried out from a car per day. All resightings of individually marked birds were recorded. We consider that if a collared bird was present, it is extremely likely to be detected at least once during the course of the day, but absolute resighting probabilities varied with time. In all years, many of the collared individuals disappeared during the middle of the staging areas from the hayfields at the College, many to feed on the adjacent wetland areas. These birds generally returned to the College fields after short periods. In addition, throughout this period, searches were also carried out throughout the western staging areas of Mýrar and adjacent areas, and again, resightings of birds bearing individual markings were recorded.

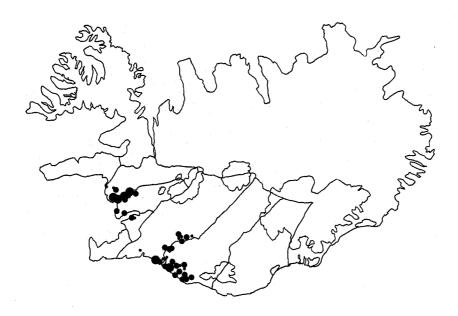


Figure 2. Geographical distribution of resightings of all individually marked Greenland White-fronted Geese, marked in Ireland, Greenland, Scotland and Iceland reported from Iceland up until I lune 1999.

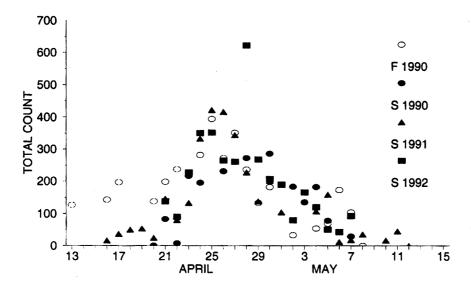


Figure 3. Counts of spring staging Greenland White-fronted Geese from regularly surveyed road transects through the southern lowlands of Iceland in the springs of 1990-1992 inclusive. Findicates a 16 km transect from Fljótshólar, Flói and S a 40 km transect from Skeið.

Results

Distribution of ringing recoveries

The distribution of all ringing recoveries of Greenland White-fronted Geese in Iceland is shown in Figure 1.All but six of these recoveries come from the autumn period. Of those remaining, four were shot illegally in spring and two were found long dead in summer. The overall distribution closely resembles that described for the spring migration reported by Francis & Fox (1987), with the majority occurring in the southern lowlands (defined here as Árnessýsla, Rangárvallassýsla and Vestur-Skaftafellssýsla) and the western lowlands (defined here Kjósarsýsla, as Borgarfjardarsýsla, Mýrarsýsla Snæfellsness- og Hnappadalssýsla). In the southern lowlands, the most important areas for recoveries lie on the coast (particularly Ölfus and Flói, Árnessýsla, Holt and Landeyjar in Rangárvallassýsla, Me∂alland in Vestur-Skaftafellssýsla), although recoveries come from areas below 200 m up to 60 km inland in Laugadalur and Biskupstungur (Árnessýsla). In the west, recoveries are most frequent about Borgarfjördur, with concentrations in the Hvítá and Andakílsá valleys (Borgarfjarðarsýsla), the low-lying boggy landscapes of Mýrar (Mýrarsýsla) and in the south eastern part of Snæfellsness peninsula (Snæfellsness- og Hnappadalssýsla). Isolated recoveries come from the western and northern valleys (Figure 1).

Distribution of resightings of marked individuals

The distribution of all resightings of individually marked Greenland White-

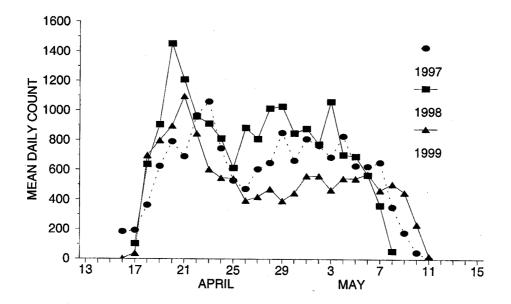


Figure 4. Counts of spring staging Greenland White-fronted Geese from Hvanneyri Agricultural College, western Iceland based on surveys of all fields and adjacent marshes in the springs of 1997-1999 inclusive. Daily data points represent the mean of all counts (minimum two, but generally three, counts per day).

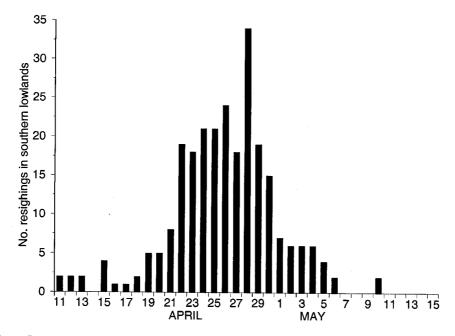


Figure 5. Distribution of the daily number of resightings of individually marked Greenland White-fronted Geese reported from the southern lowlands of Iceland during the springs of 1980-1999.

fronted Geese is shown in Figure 2. These show considerable similarity to the patterns of recoveries in their concentrations in the southern lowlands and the lowlands of western Iceland (cf. Figure 1) despite the more restricted observer coverage, which inevitably has concentrated search effort in areas known from other sources to be of importance for White-fronts.

Timing of spring migration based on counts

The counts of Greenland White-fronted Geese from the southern lowlands are shown in Figure 3. Although there were over 100 geese in Flói on 13 April 1990, the major arrival in Skeið was between 20 and 25 April in all years during 1990-1992. Peak numbers occurred on 25 April in all but the Skeið transect in 1992 (which showed a high peak of over 600 geese on 28 April), and numbers then declined throughout late April and early May. Very few Greenland White-fronted Geese were reported after 8 May in any year (Figure 3). In contrast, the counts from Hvanneyri show a rapid build up during 16-21 April during 1997-1999 (Figure 4), followed by a trough in numbers around 25 April, after which there was a modest increase in numbers which was sustained until c.6 May, when there followed a rapid and synchronous departure. Few Greenland White-fronted Geese were present after 10 May.

Timing of spring migration based on resightings of marked individuals

The daily distribution of resightings in the southern lowlands (Figure 5) and the western lowlands (Figure 6) resemble the

respective census counts, despite the fact that resighting effort was far more extensive in the two areas than just the census routes. Hence, the peak in resighting frequency in late April in the southern lowlands combined coincides with the peak numbers counted on the Skei ∂ transect. In contrast, the resightings from the western lowlands shows a bimodal distribution, with an early peak around 22 April, lower frequency of resighting to the end of the month and a peak in early May. Much of this early May peak is explained by differential effort on I May expended in the last ten years to visit Hvanneyri specifically to resight individually marked birds at this site. Nevertheless, relatively more marked geese have been reported in this phase, even accounting for this disproportionate effort on that date (Figure 6).

Timing of autumn migration based on recoveries and resignatings

Because there are relatively large numbers of recoveries of ringed geese, but few resightings (compared with the frequency of reporting in spring), the information relating to the timing of autumn staging offers less precision about when birds stage in Iceland on the return to the wintering grounds. Recoveries have been reported from 30 August to 31 October, but the majority came from the period 23 September to 15 October (Figure 7). Resightings occurred significantly later (Mann-Whitney U-test, W>1000, P < 0.001) with none reported before 23 September (reflecting lack of observer effort), and the majority of these records confined to the first half of October (Figure 7), although with some reported until 28 October.

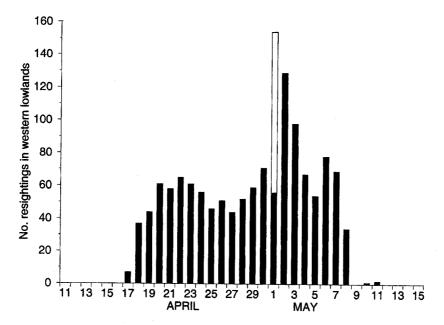


Figure 6. Distribution of the daily number of resightings of individually marked Greenland White-fronted Geese reported from the western lowlands of Iceland during the springs of 1980-1999. Note the white histogram column for I May differentiates the resightings from Hvanneyri Agricultural College where counts and searches for ringed birds have been carried out every year since 1989 on this date, and over-inflate the total for this date.

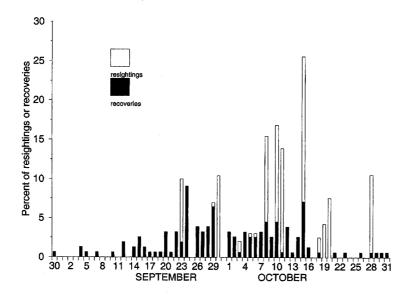


Figure 7. Distribution of the daily number of recoveries (solid columns) or resightings (blank columns) of all individually marked Greenland White-fronted Geese reported from all of Iceland in autumn.

Individual staging periods of geese in certain areas

The presence of observers counting geese at Hvanneyri at least three times per day during the springs of 1997, 1998 and 1999 gives the opportunity to see how individual birds use this site. The plot of cumulative arrivals (Figure 8) shows that in all years over 50% of all individually marked birds seen in any one season had arrived by 19 April (ie within four days of the arrival of the first geese). Nevertheless, marked geese continue to arrive at Hvanneyri into early May, and characteristically, in all three years, new individuals after the dip in numbers around 25 April. The plot of cumulative departures (based on the last dates marked individuals were reported, see Figure 8) shows individual geese leaving

very soon after arrival, but generally geese departed from 30 April, usually culminating in a rapid departure towards the end of the staging period. The frequency distribution of length of stay in all three years shows a bimodal distribution, with many staying one or two days and more than half staying for less than a week (Figure 9). Nevertheless, more than one third of birds stayed for more than two weeks, many of these remaining for the majority of the length of the entire staging period in any one year. It would therefore appear that the geese using the Hvanneyri staging area comprised many individuals which stage briefly before movement onward to other areas during the early phase of the migration period, with others remaining for the entire spring staging period. There is also some evidence for a second flush of short-staying birds which

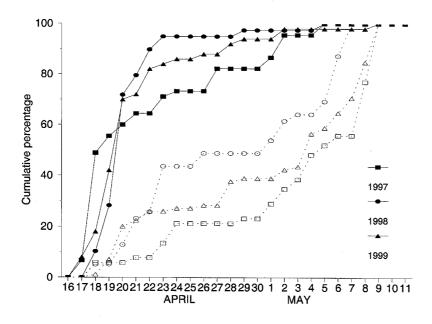


Figure 8. Patterns of arrival (solid symbols, solid lines) and departure (open symbols, dotted lines) amongst all Greenland White-fronted Geese seen at Hvanneyri Agricultural College in the springs of 1997-1999 inclusive. Data are expressed as the cumulative percentage of all individually marked birds reported in any one season that arrived or departed on a given date.

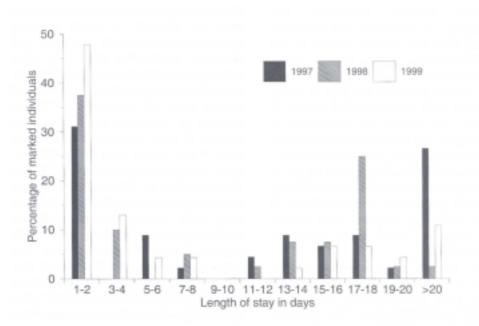


Figure 9. Annual frequency distributions of length of stay amongst individually marked Greenland Whitefronted Geese staging at Hvanneyri Agricultural College in the springs of 1997-1999 inclusive. Data relate to 40, 40 and 44 individuals respectively in 1997, 1998 and 1999.

arrive at Hvanneyri in early May (presumably having staged elsewhere) before departing for Greenland. Whether these birds originate from local staging areas or even the southern lowlands remains obscure.

Discussion

Timing of spring and autumn staging

The combination of ringing recoveries, resightings of individually marked birds and regularly counted census routes presented in this analysis suggest that Greenland White-fronted Geese stage in Iceland from c.10 April until c.12 May in spring and

c.30 August until c.31 October in autumn. The greater search effort in spring, based upon six years of investigations spanning the known staging period has inevitably meant that the timing of spring passage is better known than that of autumn. We still know very little about the precise timing of the autumn migration, its duration and the distribution of birds. Certainly it is much more difficult to see Greenland White-fronted Geese in the autumn because of the open season, which makes geese more wary and observation more difficult. Hence studies of autumn migration staging in Iceland remain a priority for the future. The results presented here confirm the importance of the southern and western lowlands of Iceland as the major staging areas for this population in spring and

Reports, recoveries and resightings of Greenland White-fronted Geese from the western sectors of the northern valleys suggest that in recent years a few birds may be using these areas on a regular basis, but numbers in spring are very small, and only survey work in autumn will confirm the importance of these areas. No attempts have been made to survey Me∂alland, Landbrot and Alftaver in Vestur-Skaftafellssýsla, known to be of some significance for White-fronted Geese in spring and autumn, and exploration of these, and other potential areas further east along the south coast remains a survey priority.

The intensity of observations in the spring from the major areas does provide some basis for examining patterns in staging phenology there. The apparent differences in the pattern of spring migration in the southern lowlands compared to the western lowlands (based on the count data) need some interpretation. The census route censused in Skeid was part of a project designed to monitor pre-nesting feeding in Pink-footed Geese and was not considered particularly representative of habitat exploited by Greenland White-fronted Geese. The census route is at least 30 km inland, yet Greenland White-fronted Geese are most abundant on the coast in the southern lowlands (Fox et al. 1992). Hence, the relatively late arrival of birds on the Skei ∂ transect could relate to their gradual movement inland from the more heavily exploited areas on the coast (eg in Landeyjar, Holt and Flói). This was confirmed to some extent by the later arrival here compared to the numbers present along the Flói transect before 17 April 1990. It is unfortunate (but unavoidable) that the transect data from the two staging areas were gathered in

different years, since comparisons between them are difficult. It would certainly appear that, in the both the Skeia and Hvanneyri count data, there is a rapid build-up of numbers to a spring migration peak, with relatively high numbers counted over a brief 4-5 day period. This is followed by a decline, but with a core number of birds remaining into the first week of May. In the years 1990-1992, the major arrival in Skeið was between 20 and 25 April, whilst in 1997-1999, it occurred at Hvanneyri during 16-21 April. In these latter years, the arrival period followed very rapidly (ie within 1-2 days) after birds departed from Wexford. Hence the differences between the two sets of data may well relate to the timing of departure from the wintering areas rather than differences between the two staging areas. However, if the patterns are consistent, it could be that the birds using the southern lowlands depart slightly earlier than those in the west. This may have some significance for linkage between the two areas, since some individually marked geese characteristically appeared at Hvanneyri late in the spring season for a short period. These individuals may have staged elsewhere (including the southern lowlands) before appearing in the west. Synchronous observations in the two staging areas are required to confirm such a linkage.

Length of stay of individual birds

The general pattern of bird use of staging areas obviously reflects the staging behaviour of individuals. Our repeated resightings of marked geese at the Hvanneyri site throughout the staging episode show that birds are using a range of differing stopover strategies at this

particular site. A large number of individuals were only ever seen once, and over half stayed at this apparently very attractive site for less than one third of the 24 day staging period. Some of these geese moved to other staging sites in the vacinity. Most were never seen again and probably moved on within Iceland, but some may even have continued on to Greenland. Most of these short-staying birds were concentrated in the early arrival phase and the final departure phase. Nevertheless, over one third of all followed individuals remained at Hvanneyri for virtually the entire duration of the staging period, arriving with the first individuals and departing amongst the later birds to leave.

These patterns of behaviour of individual birds give some insight into the patterns of turnover observed in the different areas. It would seem that there is an aggregated arrival in some areas, followed by a rapid dispersal, much of which is almost certainly local in nature, but could also include the onward passage of individuals to Greenland. The first Greenland Whitefronted Geese arrive in west Greenland in the last few days of April and in early May. During detailed studies in 1979, the first birds were observed in Greenland on 7 May and peak arrival was considered to be 12 May (Fox & Madsen 1981). In 1984 (a very late spring in Greenland) the first geese were observed on 6 May and migration intensity peaked on 8 May (Fox & Ridgill 1985). It is not clear whether the short-stayers seen during the arrival phase move on rapidly to Greenland or merely disperse to other staging sites in Iceland. Do birds in condition to breed (having attained suitable nutrient store thresholds) trade off the benefits of remaining in Iceland to stage longer (and acquire further stores) with the costs of delayed

first egg dates that come from a delayed departure to the breeding grounds? Does the delayed thaw that typifies northern elements of the breeding range of the Greenland White-fronted Goose mean that geese that breed in the north of the range remain later in Iceland than those which summer in the south (where spring conditions are more favourable to early breeding)? Alternatively, do geese simply move within Iceland in response to local feeding conditions and depart when the weather conditions dictate? We know surprisingly little about such decisionmaking in such a long-distance migratory goose population.

What is clear, is that we learn relatively little from the observations of the "average" goose in this respect, especially when that organism is a long-distance migratory bird. It would be remarkable if all 33.000 Greenland White-fronted Geese scattered across 60 different wintering sites all left for Iceland together at the same moment in spring and showed the same staging behaviour in Iceland before departing onwards to the breeding grounds. The results presented here suggest that the spring migration of this population of geese through Iceland represents a trickle rather than a flood. To be able to understand the patterns in time and space we observe, we need to determine the behaviour of the individuals that make up the population. The patterns of migration in time and space are defined by the result of a great many individual decisions, not a collective one. In this respect, we can learn a great deal from observations at one point of how and when individuals pass that particular site. Over a series of years, the accumulation of data relating to individuals can also show the regularity of their specific staging areas in time and space. Yet more can be gained

by synchronous observation at several positions throughout the staging areas, to see how much of the transitory element at each site turn up at other sites, based on individually marked geese. However, it is clear that the maximum information is to be derived from the instantaneous observations of individuals throughout a staging episode that only the use of satellite telemetry can provide. It is important to understand the energetic consequences of spring staging in Iceland in order to understand something of the that affect the breeding productivity of this population of geese. Similarly, we know nothing about the importance of this stop-off during their autumn migration to the wintering areas. If we are to both understand the nutritional consequences of these events and be in a position to offer conservation advice that can affect these factors, it is vital that we understand the staging behaviour of individual geese. Such understanding can only come from the use of new telemetry techniques combination with our existing methods.

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