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## Staging site fidelity of Greenland White-fronted Geese *Anser albifrons flavirostris* in Iceland

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**Capsule** Based upon resighting histories of marked individuals, a high level of site loyalty was found for Greenland White-fronted Geese staging in Icelandic stopover areas in spring and autumn.

**Aims** To determine levels of within- and between-season staging site fidelity, to assess whether offspring adopt the staging areas of their parents and to determine relationships between Icelandic staging areas and winter provenance of individuals.

**Methods** Sequential resighting histories and recoveries (2658 observations) of 415 different individually marked geese were analysed from the period 1986–99.

**Results** In spring, >90% of goslings associated with parents and siblings and all goslings were subsequently seen <4 km from where they were first sighted with parents in spring. Ninety-six percent of all multiple within-spring resightings of 192 marked individuals were within 4 km of each other; three geese moved 88 km from the southern to the western staging areas. Four percent of the 45 marked geese seen in two consecutive springs and none of the 27 birds seen in consecutive autumns moved more than 4 km between years. By contrast, significantly more (12%) moved greater than 4 km in subsequent seasons between spring/autumn ( $n = 56$ ) and autumn/spring ( $n = 49$ ). All these individuals shifted to Hvanneyri Agricultural College in autumn, the only declared hunting-free area for Greenland White-fronted Geese. Based upon resighting histories and recoveries of shot birds, Scottish wintering birds were more likely to use southern staging areas, and Wexford (Ireland) wintering birds were generally more likely to be seen staging in the western lowlands in Iceland.

**Conclusions** Given the apparent cultural reinforcement of patterns of use of staging areas in Iceland, the high levels of site loyalty and the relatively limited exchange between southern and western staging areas, we argue for strategic refuge designation throughout both staging areas to protect the population.

Greenland White-fronted Geese *Anser albifrons flavirostris* stage in Iceland in spring and autumn en route to and from their breeding areas in west Greenland from wintering areas in Ireland and the United Kingdom (Fox *et al.* 1999a, 1999b). They utilize two main areas, the southern lowlands (Árnessýsla, Rangárvallassýsla and Vestur-Skaftafellssýsla) and the western lowlands (Kjósarsýsla, Borgarfjardar-sýsla, Mýrarsýsla and Snæfellsness- og Hnappadalssýsla) from c. 10 April to c. 13 May and c. 30 August to 31 October. The distribution of Icelandic resightings of individually marked

geese (caught mostly in Ireland) has already been described (Fox *et al.* 1999b). To assess the significance of staging in Iceland and patterns of site-use, we need to understand how individuals use different sites. Here, we use sequential resighting histories of individually marked geese to determine levels of within-season movement. If individuals remain at one site or in the same general area, we may then have some confidence in using single observations to compare individual use of sites between years, especially site fidelity to staging sites in subsequent years. We can also address whether individuals use the same sites in spring as in autumn or if there is any relationship between the two major

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Icelandic staging areas and the breeding or wintering grounds of individual geese. Greenland White-fronted Geese show unusually long parent–offspring relationships (Warren *et al.* 1993); hence, offspring may adopt the staging areas used by their parents. In autumn, the Greenland White-fronted Goose is a legitimate quarry species in Iceland where 3000 are shot annually (Wildlife Management Institute 1999). We therefore consider whether hunting disturbance in autumn affects site-use of collared birds. It might be expected that geese using spring staging areas which are heavily hunted in autumn may show less spring–autumn and autumn–spring site-tenacity than geese using a spring staging site that is protected from hunting in autumn.

## METHODS

Data used in this analysis were collected in a number of ways from different sources. We combined opportunistic and systematic resightings of colour-ringed birds (1986–99), detailed studies at Hvanneyri College and reports of recovered birds shot during autumn migration.

### Mark-resighting database

Since 1983, 1897 Greenland White-fronted Geese have been captured and released with engraved plastic collars and/or leg rings as well as standard ringing scheme metal leg rings (Table 1). These have generated over 47 000 resightings from over 200 observers throughout their annual range to the end of May 1999. The Icelandic records of these individually marked birds consist of 2658 observations of 415 different individuals on 156 dates at 70 different sites. We define a 'site' as a separate farm or other land holding as defined on the 1:100 000 scale Landmælingar Íslands maps of Iceland. In addition, 174 marked geese have been recovered and reported as dead from Iceland, most were shot, three destroyed, two found dead and one ring only

found. These recoveries came from 108 different sites; most sites have yielded one (73 sites) or two (23) recoveries. Four sites have produced larger numbers: Bóndhóll (Mýrarssýsla 64°31'N 22°06'W) and Thykkvibær (Rangárvallassýsla 63°45'N 20°37'W) with seven recoveries each, and Leirulækjarsel (Mýrarssýsla 64°35'N 21°50'W) and Kolvidarnes (Snæfellsness- og Hnappadalssýsla, 64°48'N 22°27'W) with eight recoveries each.

### Resighting effort

The resighting effort has not been constant. Systematic spring surveys in the Andakílsá area of Borgarfjörður in western Iceland on 1 May have been undertaken by JÓH, ÓE and others (1989–99), centred on the fields and marshes of the Hvanneyri Agricultural College (Borgarfjardarsýsla, 64°34'N 21°46'W). During expeditions to study Greenland White-fronted Geese in spring and autumn 1986 (Francis & Fox 1987) and Pink-footed Geese *Anser brachyrhynchus* during the springs of 1989–92, reports of individually marked Greenland White-fronted Geese were gathered by field teams. Goose numbers were counted throughout the entire lowlands on a regular basis and along defined census routes driven daily, primarily to monitor changes in numbers of Pink-footed and Greylag Geese *A. anser*. We counted Greenland White-fronted Geese along two road transects in the southern lowlands: (1) a 40-km route in Skeid, Árnessýsla (see Fox *et al.* 1992, 2000 for precise location) driven at approximately the same time on as many dates as feasible during 12 April to 6 May 1990, 16 April to 3 May 1991 and 22 April to 10 May 1992 and (2) a 15-km transect from Fljóts-hólar (63°47'N 20°48'W) to Villingaholt (63°53'N 20°45'W) in Flói, Árnessýsla during 12 April to 6 May 1990. From 29 April to 6 May 1990, A.J.W. made daily observations at the Hvanneyri Agricultural College. In recent years, resightings of individually marked birds

**Table 1.** Place and timing of capture of individually marked Greenland White-fronted Geese that form the basis of resightings in Iceland used in this analysis.

Capture area	Time period	Number fitted with plastic collars and leg rings	Number fitted with leg rings only
Wexford, Ireland	1983–99	1303	56
Elsewhere in Ireland	1987–96	67	0
Islay, Scotland	1990–98	36	14
Lancashire, England	1992	0	1
Hvanneyri, Iceland	1997–99	72	0
Greenland	1979–97	156	192
<b>Totals</b>		<b>1634</b>	<b>263</b>

have been reported by many Icelandic observers, most notably by Gudni Sigvaldason who since 1994 has made frequent (latterly daily) observations in Pykkvibær, Rangárvallassýsla.

### Detailed studies at Hvanneyri

During the springs of 1997–99, detailed ecological studies of staging geese were undertaken at Hvanneyri Agricultural College. Observers were present during 17 April to 9 May 1997, 18 April to 7 May 1998 and 15 April to 10 May 1999. On the college farm, counts of all fields and the adjacent intertidal marshes (dominated by *Carex lyngbyei*) were carried out on a daily basis, with a minimum of three counts carried out from a car each day. Also, throughout this period, intermittent searches were made throughout the western staging areas of Mýrar and adjacent areas, resightings of birds bearing individual markings being recorded.

### Statistical analyses

A frequency distribution of distances moved by marked geese within seasons was bimodal: all moved either less than 4 km or more than 15 km, if they were reported from different sites. We define movement as only those where reports of birds were from sites more than 4 km apart. Many marked individuals have been reported staging in Iceland in several seasons from different years. In order to avoid pseudo-replication, we have only used a single sighting chosen at random when considering within-season movements of individual geese and the relationship of staging area to preceding wintering areas. Nevertheless, since some birds have been seen on a regular basis over several years, data from several successive migration events for single individuals have been pooled for comparison, but not subjected to statistical analysis.

### Recoveries of geese

Of 160 marked Greenland White-fronted Geese recovered in Iceland, previous resightings showed that 122 wintered at Wexford, 11 in the rest of Ireland, 17 on Islay and 10 in the rest of Scotland. For each wintering area, we compared the observed distribution of recoveries between the southern and western staging areas with the expected distribution based on all recoveries combined using simple chi-squared tests. Similarly, there were 351 marked individuals reported in Iceland for which the site in Ireland or Scotland used in the

preceding winter was known (these relationships were chosen at random where multiple resightings were available from more than one staging event). Of these, 296 came from Wexford, 7 from elsewhere in Ireland, 27 wintered on Islay and 21 in the rest of Scotland. The same methods were used to test whether birds from different wintering sites were similarly distributed between western and southern staging areas.

## RESULTS

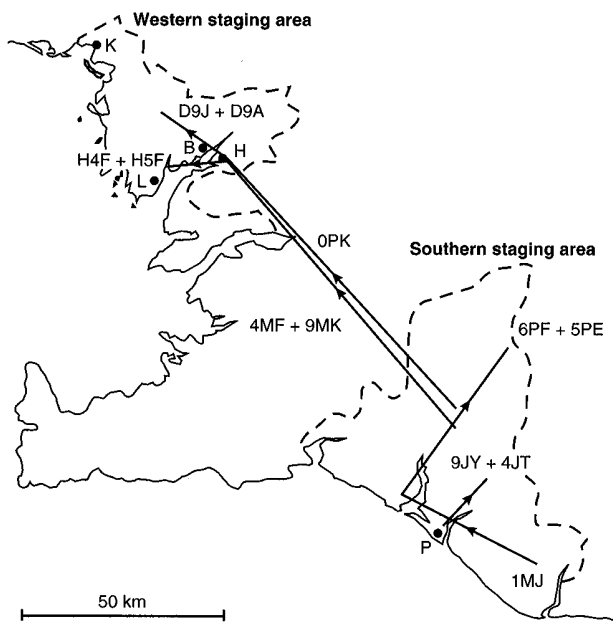
### Migration of offspring with families

No goslings ringed in Greenland have been seen during their first autumn staging episode in Iceland. Eighteen families containing at least one gosling have been seen in the goslings' first spring in Iceland. Fifteen of these families comprised all the members that had been identified on the wintering grounds, numbering 64 goslings in all. In one family, only a single gosling (of two) was identified by its collar code in Iceland and we assumed that the whole family was present. This brings the total to 66 goslings in 16 families. Of the remaining two families, two siblings were seen together in Iceland in May 1987 without their third sibling or parents, but none of these five birds was ever seen again. In the other case, 3CK was seen alone on three different occasions in Iceland in spring 1991, but was reunited with its three siblings and parents on Islay, western Scotland the following autumn. It would therefore appear that a minimum of 88% (16/18) of families remained together during spring migration and that a minimum of 90% (66/73) goslings remained with their parents for this journey.

Of these 66 goslings seen in their first spring, 21 (all in spring) have been seen and reported in subsequent years on passage in Iceland, six have also been seen in autumn. All have been reported within 4 km of the staging site where they were first seen in spring with their parents. One individual, 3XJ, has been seen in four springs and three autumns, always at the same site.

### Multiple within-spring resightings

A total of 192 geese have been reported more than once during a single spring; 79 of these have multiple resightings in more than one season, hence there are 269 'goose-seasons' with multiple resightings of individuals. Of these, 202 remained at the same staging area throughout that period, 55 involved geese making a single movement < 4 km and the remaining 12 made



**Figure 1.** Map of south and west Iceland showing movements of the 12 individual marked Greenland White-fronted Geese that moved more than 4 km between subsequent resightings during a single spring staging season in Iceland. Arrows indicate directions of movement, but not necessarily the path of travel. Codes identify individual birds. Places mentioned in the text are identified on the map: B = Bóndhóll, H = Hvanneyri, K = Kolvidarnes, L = Leirulækjarsel and P = Thykkvibær.

longer distance movements (mean 34.1 km, range 15–88 km, see Fig. 1). Three of these geese seen in the southern lowlands were later seen at Hvanneyri in the west, where all had been or were resighted in other seasons. Five geese moved westward or inland from the

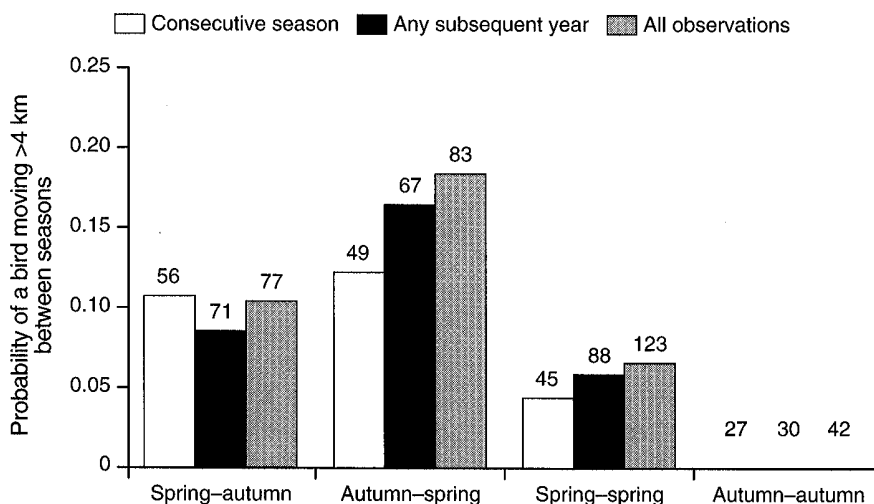
coast in the southern lowlands and four moved westwards in the western staging area. The majority (96.3%) showed no within-spring site movement. There are too few within-season multiple resightings of individuals in autumn for a similar analysis.

**Multiple between-season resightings**

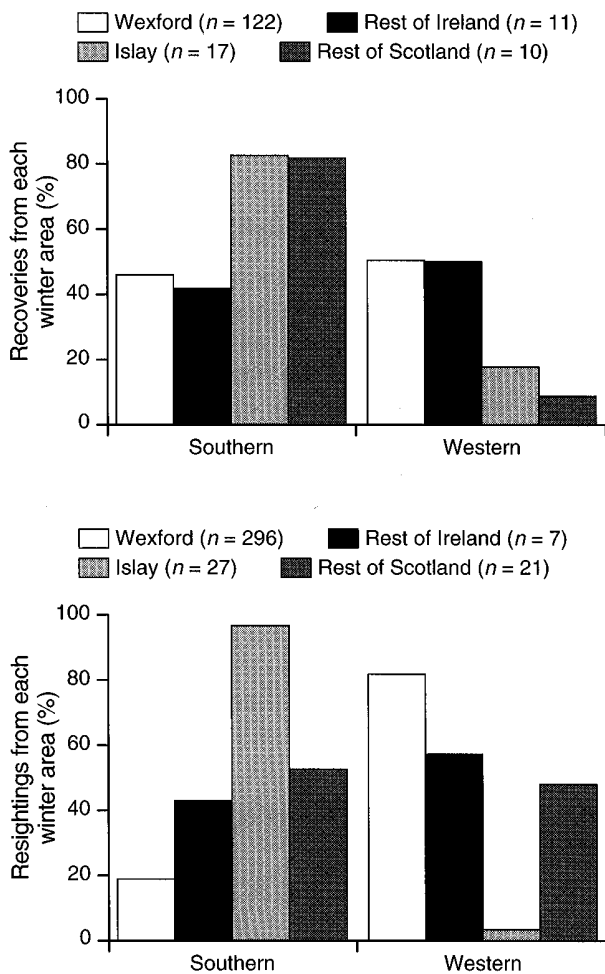
There was no significant difference between the numbers of individuals changing sites in consecutive seasons between springs and autumns (Fisher's exact probability test,  $n = 72, P = 0.38$ ), nor between spring–autumn and autumn–spring comparisons (Fisher's exact probability test,  $n = 105, P = 0.23$ ) (Fig. 2). We therefore pooled data from spring–spring and autumn–autumn to estimate the probability of same-season staging site fidelity and spring–autumn and autumn–spring to estimate the probability of different-season staging site fidelity. Same-season site fidelity (97.2%) was significantly greater than different-season site fidelity (88.6%, Fisher's exact probability test  $n = 177, P < 0.05$ ). All birds that changed staging site were seen at Hvanneyri in western Iceland during autumn.

**Relationships between wintering areas and staging areas in Iceland**

The distribution of birds of different wintering provenance is summarized in Fig. 3. Data are divided into recoveries of birds (mostly shot) and resightings of collared individuals. There were 167 recoveries of geese in Iceland in autumn for which the wintering prove-



**Figure 2.** Probability that marked Greenland White-fronted Geese use different staging areas (i.e. sites more than 4 km apart) in subsequent spring- or autumn-staging and spring–autumn or autumn–spring episodes. Data are presented on the basis of selecting one random record for each marked individual (consecutive season or any subsequent year) or using all available observations.



**Figure 3.** Wintering site origins of Greenland White-fronted Geese using the two major staging areas in Iceland, the southern and western lowlands (see text for precise definitions), as determined from recoveries ( $n = 160$ ) and resightings ( $n = 351$ ).

nance was known in the winter preceding recovery. There was no significant difference between the recovery distribution (i.e. between southern and western staging areas) of Islay wintering birds versus those wintering elsewhere in Scotland ( $\chi^2 = 0.14$ ,  $df = 1$ ,  $P = 0.72$ ), nor between Wexford wintering birds and those wintering elsewhere in Ireland ( $\chi^2 = 0.02$ ,  $df = 1$ ,  $P = 0.89$ ). Hence, the data were combined into Irish- and Scottish-wintering birds. Irish wintering birds showed no significant difference in the probability of recovery between southern and western staging areas ( $\chi^2 = 2.18$ ,  $df = 1$ ,  $P = 0.14$ ), but Scottish-wintering birds were more likely to be recovered in the southern lowlands ( $\chi^2 = 10.73$ ,  $df = 1$ ,  $P < 0.01$ ).

There were significant differences between the Iceland staging distribution of Islay, other Scottish,

Wexford and other Irish wintering geese amongst resighting data ( $\chi^2$  values were greater than 2.6 for all comparisons,  $df = 1$ ,  $P < 0.05$ ). Wexford wintering birds were more likely to be resighted in the western staging area ( $\chi^2 = 10.8$ ,  $df = 1$ ,  $P < 0.01$ ) and Islay wintering birds in the southern staging area ( $\chi^2 = 65.6$ ,  $df = 1$ ,  $P < 0.001$ ). Birds wintering elsewhere in Scotland were significantly more likely to be seen in the southern lowlands ( $\chi^2 = 6.8$ ,  $df = 1$ ,  $P < 0.01$ ). Birds from the remainder of Ireland were equally likely to be resighted in both staging areas ( $\chi^2 = 0.9$ ,  $df = 1$ ,  $P > 0.05$ , although sample sizes were small,  $n = 7$ ).

## DISCUSSION

Of marked Greenland White-fronted Geese reported more than once in a spring staging episode, 96% were reported within 4 km. This is similar to the situation in winter, where the annual probability of a marked Greenland White-fronted Goose showing within-winter changes in site-use was less than 3%, and most of these were restricted to birds staging en route to or from ultimate wintering areas (Warren *et al.* 1992). The geese that did show changes in staging site-use within Iceland were observed on the southern coast of Iceland, presumably first landfall for all geese arriving from Britain and Ireland in spring. All were subsequently reported either further inland or, in three cases, on the western staging areas, which represented their traditional staging area, based on previous and/or subsequent reports.

Since 90% of goslings resighted in Iceland during their first spring migration back to the breeding grounds remained with their parents, it appears that the use of staging areas is reinforced through extended parent-offspring relationships. The one instance where a lone juvenile was reunited with its family in a subsequent winter suggests that separation of family members at some stage on spring migration may not always result in family break-up. These associations are known to continue for up to 8 years in this population (Warren *et al.* 1993). All subsequent resightings of these goslings were reported from the same site in following springs and autumns, confirming that geese tend to adopt the staging areas of their parents, even after family break-up had occurred. Birds that are known to have paired and dissociated from their parents and siblings on the wintering grounds have been seen in the same staging area in Iceland at the same time as these family members, without showing any sign of social interaction (unpubl. data).

Only 4% of geese seen in consecutive springs and none of the 27 birds seen in consecutive autumns were reported more than 4 km apart. These are higher levels of between-season site fidelity than reported on the wintering grounds, where 8–14% of geese changed site in consecutive winters (Wilson *et al.* 1991, Warren *et al.* 1992). However, since many of these returned to their original wintering site after one year, net emigration was actually much lower. By contrast to the high level of same season fidelity in consecutive years, significantly more (11%) birds changed staging site between spring/autumn and autumn/spring. The Greenland White-fronted Goose is legal quarry in Iceland in autumn and since it stages in the lowland farms of the south and west close to centres of human population, it is a popular species for hunting. Because of its relative scarcity, only c. 3000 Greenland White-fronted Geese are shot each year in Iceland (Wildlife Management Institute 1999), but hunting is permitted anywhere in the lowlands where wildfowling have a right to shoot on private land. The one situation where the population is protected in autumn is the voluntary hunting ban declared at Hvanneyri Agricultural College in Borgarfjörður. All the geese showing spring/autumn and autumn/spring shifts in staging area moved to or from Hvanneyri in autumn, having been seen elsewhere in the preceding or following spring. This suggests that the lower level of site fidelity may be linked to modifications in behaviour that could be brought about as a result of hunting disturbance, which is known to affect the numbers of birds using staging areas (Madsen 1998a, 1998b). Support for this comes from the fact that many more geese stage at Hvanneyri in autumn than in spring (when up to 1400 stage there, Fox *et al.* 1999b, B. Thorsteinsson pers. comm.).

Two groups of hypotheses have been proposed to explain site fidelity in birds (Greenwood & Harvey 1982, Weatherhead & Forbes 1994) which invoke ecological (return to familiar sites with prior knowledge of an area offers fitness benefits over exploration of the unknown) or genetic explanations (philopatry enhances mating with individuals sharing a specific level of relatedness). There is much evidence to suggest that White-fronted Goose families tend to migrate between wintering and breeding areas together (see above). Furthermore, many species of long-term monogamous waterfowl pair outside of the summer period (although this remains unconfirmed in Greenland White-fronted Geese; Warren *et al.* 1992); hence, the genetic explanation is unlikely to play a role in this population in which individuals apparently

rarely, if ever, pair on Icelandic staging areas. Hence, it seems more likely that the prior knowledge of a staging area forms the basis for adoption of the strategy. Familiarity with a staging area brings a prior knowledge of food resources and predation risk, which are considered amongst the more plausible explanations for the high levels of breeding and wintering site fidelity observed in waterfowl species (Rohwer & Anderson 1988, Robertson & Cooke 1999). For Greenland White-fronted Geese staging in Iceland, this implies knowledge of patchily distributed feeding resources and levels of intra-specific competition. The population traditionally fed upon the over-wintering below-ground parts of *Carex lyngbyei* and *Eriophorum angustifolium* which typically grew in the natural and semi-natural wetlands of southern and western Iceland (Gardarsson 1975, Francis & Fox 1987). There is evidence that such food sources are eaten out after periods of exploitation (at least on the wintering grounds, D.A. Stroud pers. comm.). Indeed, local plant populations may take one or two years to recover from goose exploitation before they provide a profitable food resource again (Hupp *et al.* 2000). Knowledge of several such feeding sites in one staging area would be necessary to sustain individuals over several seasons. Staging site fidelity may also confer an advantage in terms of a safe roost site, knowledge of predator densities and predator habits. In this way, staging geese are likely to become associated with safe overnight roosts and a set of daytime feeding areas in the vicinity.

In the last 1000 years, human activities have greatly changed the nature of the Icelandic lowland landscape. However, it is only in the last 60 years that extensive creation of dry hayfields and the draining of wetlands has taken place on a large scale in a manner likely to affect the White-fronted Geese (Francis & Fox 1987). In recent decades, spring staging Greenland White-fronted Geese in Iceland have increasingly used managed grasslands for food (Fox *et al.* 1998, 1999b) and their reliance on wetlands has decreased. Nevertheless, since farms were associated with wetlands (which in former times provided food for over-wintering livestock in the form of hay made from *Carex lyngbyei*), the creation of grass-sward hayfields in the vicinity of farms provides an alternative source of food for geese with established patterns of use for roost and feeding areas. The geese stage in Iceland in spring for 2–3 weeks – even if they encounter inclement weather during this stay, they have a prolonged period in which to accumulate fat and protein stores in preparation for the migration across the Greenlandic ice-cap



to the breeding areas on the west coast (Fox *et al.* 1999b, Glahder *et al.* 1999). We may therefore be witnessing a staging strategy evolved in response to a patchy wetland resource that persists in a predominantly agricultural landscape today. This is apparently in contrast to the flexible response of Pink-footed Geese staging in northern Norway, where recent changes in spring staging behaviour have included colonization of novel habitats. This population of Pink-footed Geese has had to adjust to recent changes in agricultural patterns and to active and intense scaring programmes during spring migration in very recent years. Rather than showing site fidelity, these Pink-footed Geese changed their northwards migratory patterns in response to previous experience and prevailing weather/feeding conditions in any particular season (Madsen *et al.* 1997, 1999). By contrast, the Greenland White-fronted Geese staging in Iceland have, so far, only had to adapt to the shift from natural wetland habitats to feeding on adjacent agricultural grasslands.

Why are changes in staging sites so rare? Obviously, this may in part be due to the bias in patterns of observation involved in this study – it has been impossible to cover all staging areas adequately during all migration periods. However, the population exhibits extended parent–offspring associations and high rates of mate fidelity (Warren *et al.* 1993, Black *et al.* 1996). Hence, it would be expected that the switch from using the staging area of parents to the staging area of a new mate after the point of pairing would be an event occurring generally only once in the lifetime of an individual. This means that, on an annual basis, the probability of a site change associated with the pairing of two birds using different staging areas occurring and being detected amongst the marked individuals is quite low. Equally, the concentration of search effort at relatively few sites in Iceland ensures a disproportionately high probability of detecting site-loyal individuals. The application of modern capture–mark–recapture techniques (e.g. White & Burnham 1999) using multi-strata models (Hestbeck *et al.* 1991) enables the estimation of transition rates between sites as a measure of site fidelity. Although the existing database for staging White-fronted Geese is not sufficiently large or robust to support such analysis at the present time, there is considerable potential in continuing the constant resighting effort at a few staging sites in Iceland over many years to generate such estimates in the future.

The data from the resightings and recoveries show that the geese staging in the south of Iceland are more

likely to winter in Scotland, while birds wintering in Wexford were more likely to be resighted in the western staging area, although Wexford birds were equally likely to be recovered in both staging areas. The reasons why Wexford geese are proportionally more likely to be recovered than resighted in the southern lowlands is difficult to determine. However, this could relate to the fact that all recoveries come from the autumn, whereas the majority of resightings were gathered in the spring staging period, when birds may be less likely to redistribute between the two staging areas. Nevertheless, the consistently high proportion of birds that winter in Scotland and use the southern lowlands suggests there is some segregation of the different elements of the population by staging area in Iceland. It has been established from ringing recoveries that Wexford and Irish-wintering birds generally occur in the north of the breeding range in Greenland (Fox *et al.* 1983) so some degree of spatial isolation (and hence genetic separation) may be maintained throughout the annual cycle.

The conclusions drawn from these analyses are subject to considerable bias in the gathering of the data. The restricted nature of the resightings in time and space probably results in an overestimation of site loyalty amongst staging birds. Similarly, the use of recoveries from shot birds inevitably introduces bias associated with the distribution and intensity of hunting activity, which is likely to provide information not representative of all areas. Nevertheless, the patterns of high levels of site fidelity and segregation of wintering elements between the two major staging areas seem well founded. The high degree of staging site fidelity and the geographical segregation of different breeding/wintering elements of the population confirms the need for the establishment of hunting-free refuges and habitat protection throughout the known staging areas in Iceland. The population is particularly subject to heavy hunting pressure along the south coast of Holt in the southern lowlands, and the geese using this area (likely to be of largely Scottish wintering stock) would benefit from the provision of a hunting-free refuge. There remains the need for an effective survey (perhaps using aerial survey techniques) to establish the precise distribution of the species staging in Iceland in spring and autumn. This would provide the basis for a full assessment of the distribution and abundance of the population which would underpin the provision of hunting-free areas in autumn and provide the basis for site-safeguard recommendations for wetland habitats still used by migrating geese.

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## REFERENCES

- Black, J.M., Choudhury, S. & Owen, M.** 1996. Do Barnacle Geese benefit from lifelong monogamy? In Black, J.M. (ed.) *Partnerships in Birds: the Study of Monogamy*: 91–117. University Press, Oxford.
- Fox, A.D., Madsen, J. & Stroud, D.A.** 1983. The summer ecology of the Greenland White-fronted Goose (*Anser albifrons flavirostris*). *Dansk Ornithol. Foren. Tidssk.* **77**: 43–55.
- Fox, A.D., Boyd, H. & Warren, S.M.** 1992. The phenology of spring pre-nesting feeding in Iceland-nesting geese. *Ecography* **15**: 289–295.
- Fox, A.D., Kristiansen, J.N., Stroud, D.A. & Boyd, H.** 1998. The effects of simulated spring goose grazing on the production and protein content of *Phleum pratense* leaves. *Oecologia* **116**: 154–159.
- Fox, A.D., Norriss, N.W., Wilson, H.J., Merne, O.J., Stroud, D.A., Sigfusson, A. & Glahder, C.** 1999a. Greenland White-fronted Goose *Anser albifrons flavirostris*. In Madsen, J., Cracknell G. & Fox, A.D. (eds) *Goose Populations of the Western Palearctic. A Review of Status and Distribution*: 131–142. Wetlands International Publication No. 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute, Rønde, Denmark.
- Fox, A.D., Hilmarsson, J.Ó., Einarsson, Ó., Boyd, H., Kristiansen, J.N., Stroud, D.A., Walsh, A.J., Warren, S.M., Mitchell, C., Francis, I.S. & Nygaard, T.** 1999b. Phenology and distribution of Greenland White-fronted Geese *Anser albifrons flavirostris* staging in Iceland. *Wildfowl* **50**: 31–45.
- Fox, A.D., Einarsson, Ó., Hilmarsson, J.Ó., Boyd, H. & Mitchell, C.** 2000. Viddöl heiddagæsa Á Sudurlandi að vori. *Bliki* **20**: 11–20.
- Francis, I.S. & Fox, A.D.** 1987. Spring migration of Greenland White-fronted Geese through Iceland. *Wildfowl* **38**: 7–12.
- Gardarsson, A.** 1975. Icelandic Wetland Birds. In Gardarsson, A. (ed.) *Wetlands*: 100–134. Icelandic Environmental Union Publication No. 4, Reykjavík (In Icelandic).
- Glahder, C., Fox, A.D. & Walsh, A.J.** 1999. Satellite tracking of Greenland White-fronted Geese. *Dansk Ornithol. Foren. Tidssk.* **93**: 271–276.
- Greenwood, P.J. & Harvey, P.H.** 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* **13**: 1–21.
- Hestbeck, J.B., Nichols, J.D. & Malecki, R.A.** 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* **72**: 523–533.
- Hupp, J.W., Robertson, D.G. & Schmutz, J.A.** 2000. Recovery of tall cotton-grass following real and simulated feeding by snow geese. *Ecography* **23**: 367–373.
- Madsen, J.** 1998a. Experimental refuges for migratory waterfowl in Danish wetlands: I. Baseline assessment of the disturbance effects of recreational activities. *J. Appl. Ecol.* **35**: 386–397.
- Madsen, J.** 1998b. Experimental refuges for migratory waterfowl in Danish wetlands: II. Tests of hunting disturbance effects. *J. Appl. Ecol.* **35**: 398–417.
- Madsen, J., Hansen, F., Kristensen, J.B. & Boyd, H.** 1997. *Spring Migration Strategies and Stopover Ecology of Pink-footed Geese: Results of Fieldwork in Norway 1996*. National Environmental Research Institute Report No. 204. NERI, Kalø.
- Madsen, J., Kuijken, E., Meire, P., Cottar, F., Haitjema, T., Nicolaisen, P.I., Bønes, T. & Mehlum, F.** 1999. Pink-footed Goose *Anser brachyrhynchus*: Svalbard. In Madsen, J., Cracknell, G. & Fox, A.D. (eds) *Goose Populations of the Western Palearctic. A Review of Status and Distribution*: 82–93. Wetlands International Publication No. 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute, Rønde, Denmark.
- Robertson, G.J. & Cooke, F.** 1999. Winter philopatry in migratory waterfowl. *Auk* **116**: 20–34.
- Rohwer, F.C. & Anderson, M.G.** 1988. Female biased philopatry, monogamy and the timing of pair formation in migratory waterfowl. *Curr. Ornithol.* **5**: 187–221.
- Warren, S.M., Fox, A.D., Walsh, A.J., Merne, O.J. & Wilson, H.J.** 1992. Wintering site interchange amongst Greenland White-fronted Geese *Anser albifrons flavirostris* captured at Wexford Slobbs, Ireland. *Bird Study* **39**: 186–194.
- Warren, S.M., Fox, A.D. & Walsh, A.J.** 1993. Extended parent-offspring relationships amongst the Greenland White-fronted Goose. *Auk* **110**: 145–148.
- Weatherhead, P.J. & Forbes, M.R.L.** 1994. Natal philopatry in passerine birds: genetic or ecological influences? *Behav. Ecol.* **5**: 426–433.
- White, G.C. & Burnham, K.P.** 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46** (suppl.): 120–139.
- Wildlife Management Institute** 1999. The Official Icelandic Annual Hunting Bag Statistics. <http://www.ni.is/veidi/veidist/enska.htm>.
- Wilson, H.J., Norriss, D.W., Walsh, A., Fox, A.D. & Stroud, D.A.** 1991. Winter site fidelity in Greenland White-fronted Geese *Anser albifrons flavirostris*: implications for conservation and management. *Ardea* **79**: 287–294.

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# APPENDIX 1.

## *Statistical Endnote*

Rather than break up the text of the graph legends, it was considered more appropriate to collate all the statistical material relating to the presented graphs in one place. There follows the statistics associated with these figures, identified by the superscript codes in the text. For ease of comprehension, all significant relationships ( $P < 0.05$ ) are highlighted by shading in appropriate boxes in the following tables.

<sup>1</sup>**Figure 3.1** Body mass determinations with capture date in winter from Wexford southeast Ireland, combining data from all years 1984-1999 inclusive.

Polynomial regressions were fitted on the basis of the simplest significant model that fitted the data and explained most variance in the analysis of variance. Mass is measured in g and t expressed in days from 1 October:

Age sex class	Regression model	R	df	F	P
Adult males	Mass = 2786 - 2.861t+0.0213t <sup>2</sup>	0.308	1,291	15.22	<0.001
Adult females	Mass = 2513 - 0.889t+0.0513t <sup>2</sup> +0.00010t <sup>3</sup>	0.436	1,269	20.80	<0.001
Juvenile males	Mass = 2507 - 1.279t+0.0151t <sup>2</sup>	0.341	1,351	22.96	<0.001
Juvenile females	Mass = 2231 - 1.630t+0.0318t <sup>2</sup> +0.00018t <sup>3</sup>	0.395	1,311	19.0	<0.001

<sup>2</sup>**Figure 4.1** Changes in body mass with capture date in Iceland, spring 1999.

Simple linear regressions were fitted. Mass is measured in g and t expressed in days from 1 April

Sex class	Regression model	R	df	F	P
Adult males	Mass = 2152.9 + 30.1t	0.515	1,29	10.48	0.003
Adult females	Mass = 2021.8 + 24.6t	0.453	1,19	4.91	0.039

<sup>3</sup>**Figure 4.2** Relationship between field score of abdominal profile and body mass at capture in Iceland, spring 1999.

Simple linear regressions were fitted. Mass is measured in g and API in standard units

Sex class	Regression model	R	df	F	P
Adult males	Mass = 2377.7 + 285.1API	0.661	1,28	21.78	<0.001
Adult females	Mass = 2210.4 + 228.8API	0.535	1,19	7.61	0.012

<sup>4</sup>**Figure 6.1** Changes in the percentage of juveniles in the autumn counts at Wexford and Islay during 1983-1999 inclusive.

Simple linear regressions were fitted on arc sine square root transformed proportion data. %J represents transformed proportion juveniles, and t is measured in years since 1982.

Wintering site	Regression model	R	df	F	P
Wexford	%J = 0.500 - 0.0120t	0.660	1,16	11.49	0.004
Islay	%J = 0.413 - 0.0024t	0.155	1,16	0.37	0.552

<sup>5</sup>**Figure 6.3** Changes in the estimated percentage of potentially breeding females returning with young in the autumn at Wexford and Islay during 1983-1999 inclusive.

Simple linear regressions were fitted on arc sine square root transformed proportion data. %F represents transformed proportion of successfully breeding females, and t is measured in years since 1982.

Wintering site	Regression model	R	df	F	P
Wexford	$\%F = 0.426 - 0.0109t$	0.711	1,16	15.3	0.001
Islay	$\%F = 0.417 - 0.0077t$	0.516	1,16	5.44	0.034

<sup>6</sup>**Figure 6.4** Changes in the estimated number of potentially breeding females returning with young in the autumn at Wexford and Islay during 1983-1999 inclusive.

Simple linear regressions were fitted. N represents number of successfully breeding females, and t is measured in years since 1982.

Wintering site	Regression model	R	df	F	P
Wexford	$N = 501.9 - 13.6t$	0.486	1,16	4.64	0.048
Islay	$N = 309.1 + 9.9t$	0.341	1,16	1.97	0.180

<sup>7</sup>**Figure 6.5** Changes in the estimated number of young produced per potentially breeding female in the autumn at Wexford and Islay during 1983-1999 inclusive.

Simple linear regressions were fitted. N represents mean number of young produced per potentially breeding female, and t is measured in years since 1982.

Wintering site	Regression model	R	df	F	P
Wexford	$N = 51.7 - 0.0258t$	0.793	1,16	12.9	0.003
Islay	$N = 14.9 - 0.0073t$	0.237	1,16	0.89	0.360

<sup>8</sup>**Figure 6.6** Changes in the proportion of annual marked cohorts (of juveniles hatched in 1983-1994 inclusive) known to have bred successfully before 1999 based on observations at Wexford during 1983-1999 inclusive.

Simple linear regressions were fitted on arc sine square root transformed proportion data. N represents transformed proportion of each cohort that has bred successfully, and t is measured in years since 1982. Using Spearman Rank Correlation Coefficient gives the same results (1983-1994  $r_s = 0.797$   $P < 0.01$ ; 1983-1991  $r_s = 0.568$   $P > 0.05$ )

Cohorts	Regression model	R	df	F	P
1983-1994	$N = 0.421 - 0.0196t$	0.749	1,10	12.8	0.005
1983-1991	$N = 0.410 - 0.0172t$	0.568	1,8	3.39	0.111

<sup>9</sup>**Figure 6.8** Changes in annual mean brood size amongst flocks in the autumn counts at Wexford and Islay during 1983-1999 inclusive.

Simple linear regressions were fitted. N represents mean brood size, and t is measured in years since 1982.

Wintering site	Regression model	R	df	F	P
Wexford	$N = 3.687 - 0.0305t$	0.482	1,16	4.23	0.050
Islay	$N = 2.600 + 0.0691t$	0.702	1,16	14.54	0.002

<sup>10</sup>**Figure 6.9** Changes in the proportion of different habitat types used (per annum) by individually marked Greenland White-fronted Geese wintering at Wexford based on observations during 1984/85-1998/99 inclusive.

Simple linear regressions were fitted on arc sine square root transformed proportion data. %C represents transformed proportion of habitat use in each year, and t is measured in years since 1983/84.

Habitat type	Regression model	R	df	F	P
Reseeded grass	%C = 1.255-0.0287t	0.777	1,14	19.84	<0.001
Stubble	%C = 0.148-0.0134t	0.430	1,14	2.95	0.110
Root crops	%C = 0.140+0.0253t	0.559	1,14	5.90	0.030
Winter cereal	%C = 0.218-0.0063t	0.226	1,14	0.70	0.419
Beans	%C = 0.0005-0.0042t	0.207	1,14	0.58	0.458

<sup>11</sup>**Figure 8.1** Relationship between annual winter hunting mortality rate (expressed as percentage of maximum count + annual kill) and overall annual adult return rate of Greenland White-fronted Geese wintering at Wexford based on observations during 1984/85-1998/99 inclusive.

A simple linear regression model was fitted on arc sine square root transformed proportion data for both parameters. R represents transformed adult annual return rate and K represents transformed annual winter hunting mortality in each year.

Regression model	R	df	F	P
R = 1.252-0.544K	0.503	1,22	6.45	0.020

<sup>12</sup>**Figures 8.3, 8.4. and 8.5** Annual survival and transition probabilities for Greenland White-fronted Goose caught at Wexford 1983/84-1997/98 - an analysis of survival and site interchange based on resightings and recoveries.

### Outline methods

*Data.* During 1983-1997, 1,255 adult and juvenile White-fronted Geese were captured and marked with neck collars at Wexford, Ireland (Table A1), generating 36,000 resightings and 194 recoveries up to October 1998. A bird must have been observed twice during a season at Wexford to be included in the data set, generating 2,182 “resightings” (or bird-years) at Wexford 1984-1997 and 323 “bird-years” from Islay (Table A1). The recovery year started on 1 October, but recoveries followed the birds’ annual cycle. Hence, a goose recovered in Iceland on 2 October 1987 was placed in the 1986/87 recovery year; but if recovered in Ireland on 28 September, it was referred to 1987/88. Ten recoveries were not used because recovery circumstances were unclear (Table A1). In 48 cases of known collar loss, birds were removed from the data set following the last date when they were observed with collar (treated as losses on capture).

*Analysis.* MARK was used for all analyses, using the Burnham (1993) recovery-recapture model and multi-stage models (e.g. Hestbeck et al. 1991). Recovery-recapture parameters were as follows: *S* (survival), *p* (resighting probability), *r* (recovery probability), *F* (site fidelity - complement of permanent emigration), and multi-stage parameters: (apparent survival), *p* (resighting probability), (transition probability, here the probability of moving between sites).

### Results

*Recovery-recapture analysis.* Goodness-of-fit of the general model ( $S_{a2^*b}, p_b, r_b, F_{a2^*t}$ ) was acceptable ( $\chi^2 = 1.10$ ), though there were indications of temporary emigration. The selected model was  $S_{a2^*b}, p, r_b, F$  (Table A2). Survival varied over time, independently for adults (range 0.50-0.88, Figure 8.3) and juveniles (range 0.23-0.83, Figure 8.4). Weighted mean annual survival was 0.678 (95% C.L. 0.632-0.720) for juveniles and 0.785 (0.762-0.805) for adults. Resighting probability *p* was 0.87, recovery probability *r* varied from 0.07-0.42 (weighted mean: 0.18) and fidelity probability *F* was 0.93, indicating 7% permanent emigration per year.

*Multi-site analysis.* No goodness-of-fit test is available for this type of model, the results from the recovery/recapture approach were used to start from model  $a2^*b, p_{c,b}, a2^*t$ . Since all birds were ringed at Wexford, no juvenile transition probability from Islay to Wexford could be estimated. No simplifications of the starting model were possible (Table 3). Apparent survival thus followed the same pattern as in the recovery-recapture analysis, and estimates were nearly identical: weighted mean annual survival was 0.667 (95% C.L. 0.627-0.705) for juveniles and 0.763 (0.745-0.780) for adults. Resighting probability *p* was constant (0.96) at Wexford and variable (range 0.28-0.82) at Islay. Transition

probabilities were variable both for juveniles and adults from Wexford to Islay and for adults from Islay to Wexford (Figure 8.5; all birds were marked at Wexford, so no juveniles were available to move from Islay to Wexford). Weighted means were: Wexford $\leftrightarrow$ Islay (adults) 0.084 (0.071-0.100); Wexford $\leftrightarrow$ Islay (juveniles) 0.127 (0.095-0.168); Islay $\leftrightarrow$ Wexford 0.176 (0.140-0.219).

**Table A1.** Numbers of Greenland white-fronted geese marked, resighted (twice at Wexford, once at Islay) and recovered 1983-1997.

Season	Marked	Resighted		Recovered
		Wexford	Islay	
1983/84	40			4
1984/85	161	21	2	12
1985/86	135	100	8	18
1986/87	95	157	15	19
1987/88	93	138	17	16
1988/89	110	183	14	10
1989/90	58	194	36	25
1990/91	83	152	23	12
1991/92	83	164	22	4
1992/93	94	170	23	15
1993/94	100	180	19	9
1994/95	69	197	37	16
1995/96	45	201	33	7
1996/97	60	161	46	11
1997/98	29	164	28	6
Total	1255	2182	323	184

**Table A2.** Model selection for the combined analysis of recoveries and resightings.

Model	QAIC	Akaike weight
$S_{a2^*t}, p, r_b, F$	0	0.767
$S_{a2^*t}, p_b, r_b, F$	3.81	0.114
$S_{a2^*t}, p, r, F$	3.92	0.108
$S_{a2^+t}, p, r_b, F$	9.06	0.008
$S_{a2^*t}, p, r_b, F_t$	11.38	0.003
$S_{a2^*t}, p, r_b, F_{a2^*t}$	32.93	0
$S_{a2^*t}, p_b, r_b, F_{a2^*t}$	114.77	0

**Table A3.** Model selection for the multi-site analysis.

<b>Model</b>	<b>AIC</b>	<b>Akaike weight</b>
$a2^{*b} p_{c,b} a2^{*t,t}$	0	0.560
$a2^{*b} p_{c,b} t,t$	0.48	0.439
$a2^{*b} p_{c,b} a2,c$	14.77	0.0003
$a2^{*b} p_{c,c} a2^{*t,t}$	21.10	0.00001
$a2^{*b} p_{c,b} a2^{*t}$	30.38	0