

The rise and fall of the Greenland White-fronted Goose:

a case study in international conservation

*Tony D. Fox, David Stroud, Alyn Walsh, John Wilson,
David Norriss and Ian Francis*

ABSTRACT Greenland White-fronted Geese *Anser albifrons flavirostris* breed in west Greenland and winter in Britain & Ireland, staging in Iceland on spring and autumn migration. The population declined from the 1950s until the 1970s, but legislation in 1982 removed hunting pressure on the wintering grounds and the population doubled to 35,600 between then and 1999. However, studies at key wintering sites suggested that factors other than hunting regulated local abundance in several cases. Since 1999, the whole population has shown widespread decline. This paper considers possible reasons for the sustained reduction in breeding output that has caused the population decline. There is no evidence for greater predation of nesting attempts, and the declining proportion of potential breeding birds that return to wintering grounds with young is probably related to female body condition and ability to reproduce. Several factors, including June weather and increasing intraspecific competition, show some correlation with falling breeding success, but none convincingly explains the trends. The arrival in Greenland of breeding Greater Canada Geese *Branta canadensis*, and the consequent interspecific competition with Greenland White-fronts, seems the most likely explanation for the population changes, but hard evidence for this on a large scale is also lacking. If the spread of Canada Geese is responsible, there are few conservation actions that could be taken to help the Greenland White-front. The autumn hunt in Iceland was not originally implicated in the recent decline, but with dramatically falling numbers it may now be important; controlling this hunt may be one feasible way to ease pressure on the population. It must be hoped that White-fronts can find a way of coexisting with Canada Geese in west Greenland, as they do throughout much of the central Canadian Arctic, although the population levels of the former will probably be lower than they were in the late 1990s.

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The dark coloration and distinctive morphology of the Greenland White-fronted Goose *Anser albifrons flavirostris* make it one of the more readily identifiable of the four traditionally recognised races of the circumpolar [Greater] White-fronted Goose *A. albifrons* (Ely *et al.* 2005). The Greenland White-front has a disjunct breeding and wintering distribution, a distinctive feeding ecology and unusual population dynamics. While only a small proportion of potential breeding birds return with young, they typically produce large families, show exceptional extended parent-offspring associations (which may persist for nine years or more; Warren *et al.* 1993) and are older than birds in most other goose populations when they first breed (Warren *et al.* 1992a).

In 1999, the recovery of the Greenland White-fronted Goose represented a conservation success story. The small, geographically restricted population had declined between the 1950s and 1970s (from 17,500–23,000 to 14,300–16,600 birds; Ruttledge & Ogilvie 1979; fig. 1), which led to protective legislation in 1982 to protect the bird from hunting on the wintering grounds (almost exclusively in Britain & Ireland; Stroud 1992). The 1980s were also a period of extensive site-safeguarding for the population, including the designation of breeding areas in west Greenland as Ramsar sites, thought to safeguard one fifth of all summering birds (Stroud 1992). Local management agreements covering several of the wintering areas were negotiated and wintering sites (especially night-time roosts) were designated as Ramsar sites and Special Protection Areas (under the EU Birds Directive, 1979) in Britain & Ireland (protecting the habitat of 59% of the British total, 28% of the whole population). The combination of hunting restrictions and site protection enabled the world population to increase from 16,500 in 1982/83 to 35,600 in 1999/2000 (fig. 1).

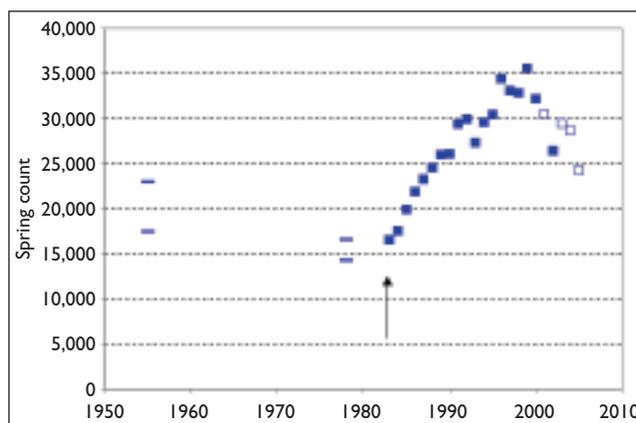


Fig. 1. Changes in estimated world population size of the Greenland White-fronted Goose *Anser albifrons flavirostris* since the population estimates of Ruttledge & Ogilvie (1979); shown here as upper and lower estimates for the 1950s and 1970s). These are based on co-ordinated spring (late March/early April) counts undertaken at all known regular localities since spring 1983. The arrow indicates the point at which the population was protected from winter hunting. Note that the missing value for 2001 (due to access restrictions during the foot-and-mouth epidemic) was estimated from a regression model predicting spring numbers from autumn counts (which explained 97% of the variance in the years 1982–2000). Missing values for 2003–2005 are estimated (because of uncollated counts from the rest of Ireland) on the basis of a regression model using total British and Wexford counts in other years (which explained 99% of the variance in the relationship between 1983 and 2000).

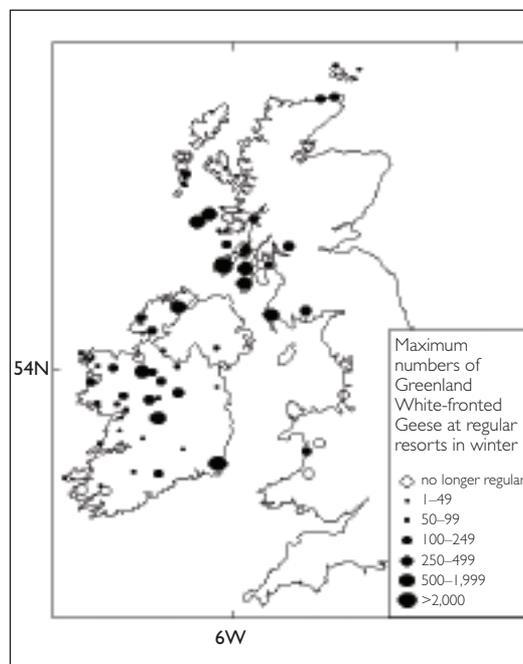


Fig. 2. Map showing the current wintering distribution of the Greenland White-fronted Goose *Anser albifrons flavirostris* in Britain & Ireland. Open symbols indicate former regular wintering sites abandoned since 1982.

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115. Greenland White-fronted Geese *Anser albifrons flavirostris* at Wexford North Slob, Ireland.

Management of hunting

The removal of winter hunting mortality was the key factor in the Greenland White-front population recovery in the 1980s and 1990s. Co-ordinated counts throughout the winter range (see fig. 2) were not available prior to 1982, when the network covering all known wintering sites was first established in Britain by the Greenland White-fronted Goose Study (GWGS; Stroud 1984) and in Ireland by the National Parks and Wildlife Service (supported by the RSPB in Northern Ireland). Subsequent counts showed increases at the two numerically most important wintering sites: Wexford Slobs in southeast Ireland and Islay in the Inner Hebrides (fig. 3). These sites, for which earlier counts also exist, have together supported approximately two-thirds of the global wintering population since 1982/83. At Wexford Slobs, retrospective analysis showed that the crude annual adult survival rate (based on census data and annual age-ratio sampling in the flocks) was negatively correlated with the size of the local Wexford winter hunting bag, indicating that the hunting kill was fully additive (see below; Fox 2003). This is important, because if restrictions on hunting are to be used as a management tool, we need to understand whether the hunting kill adds to annual mortality ('additive mortality'), or whether it is

merely 'compensatory', in the sense that the same number of birds as those shot would have died that year anyway from some other cause, perhaps some density-dependent effect (see Newton 1998, and below). The indications from the Wexford data were, however, that the kill was not removing a harvestable surplus in the population, but rather adding to natural mortality.

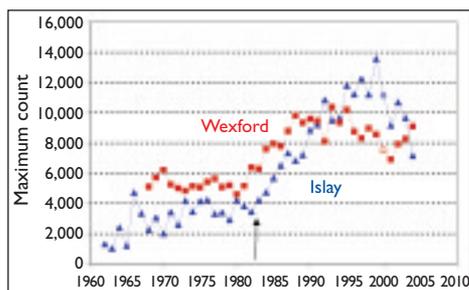


Fig. 3. Changes in maximum counts of Greenland White-fronted Geese *Anser albifrons flavirostris* at Wexford Slobs (southeast Ireland, solid squares) and Islay (Inner Hebrides, solid triangles) since regular counts began (data courtesy Parks and Wildlife Service Ireland and NCC, SNH and Dr Malcolm Ogilvie, respectively). Data for spring 2001, missing owing to foot-and-mouth disease, have been substituted with inferred values based on the regression models of previous autumn counts for both sites. The arrow indicates the point at which the population was protected from hunting on the wintering grounds.

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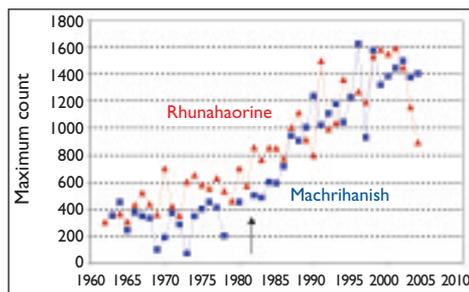


Fig. 4. Changes in maximum counts of Greenland White-fronted Geese *Anser albifrons flavirostris* in the two major flocks on Kintyre (southwest Scotland) since regular counts began. Flocks are at Rhunahaorine (solid triangles) and Machrihanish (solid squares). The arrow indicates the point at which the population was protected from hunting on the wintering grounds.

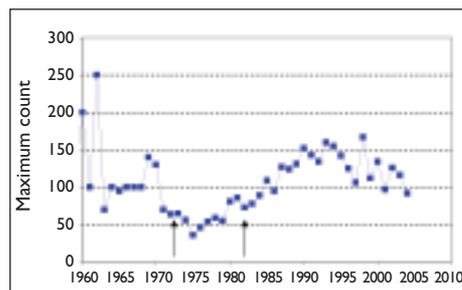


Fig. 5. Changes in maximum counts of Greenland White-fronted Geese *Anser albifrons flavirostris* on the Dyfi Estuary (mid Wales) since regular counts began. The left-hand arrow indicates the point in 1972 at which the population was protected from hunting by a local voluntary ban instigated by the local shooting club; this ban continues to the present day. The right-hand arrow indicates the point at which the population was protected from hunting on the Scottish and Irish wintering grounds.

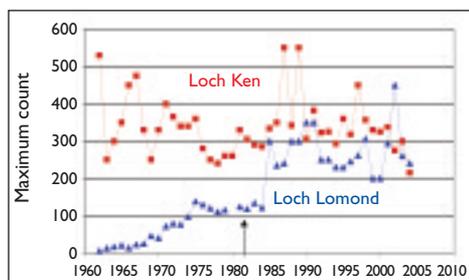


Fig. 6. Changes in maximum counts of Greenland White-fronted Geese *Anser albifrons flavirostris* at two sites in southwest Scotland – Loch Ken (squares) and Loch Lomond (triangles) – since regular counts began. The arrow indicates the point at which the population was protected from hunting on the wintering grounds.

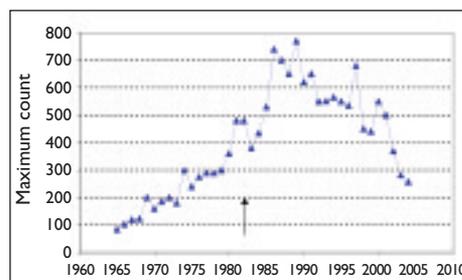


Fig. 7. Changes in maximum counts of Greenland White-fronted Geese *Anser albifrons flavirostris* at Stranraer (southwest Scotland) since regular counts began. The arrow indicates the point at which the population was protected from hunting on the wintering grounds.

It would have been tempting to conclude that here was a population which had been limited by hunting below a theoretical potential population threshold. Released from the limitation of winter shooting mortality, the population could expand to a level where overall numbers were limited by some other mechanism. However, this does not explain the changes in abundance at other wintering sites. At some key sites, Greenland White-fronts were counted every year prior to the start of co-ordinated winter counts in 1982/83. From these data, we know that numbers at some sites (Wexford Slob, Islay and two flocks on Kintyre, at Machrihanish and Rhunahaorine; figs. 3 & 4) showed no clear trends in the years prior to 1982/83 but increased following the changes in hunting legislation (Fox *et al.* 1998b). Birds at the Dyfi Estuary, in mid Wales, had shown

longer-term declines since the 1950s; this flock had been the subject of a local voluntary shooting ban since 1972 and so had shown an earlier recovery after the removal of local hunting pressure (fig. 5). These findings appeared to support the hypothesis that hunting mortality kept numbers below their potential. However, two flocks using protected lochs in southwest Scotland (Loch Ken, SSSI and part RSPB reserve, and Loch Lomond, SSSI and part National Nature Reserve; fig. 6) showed either an increase up to 1982 followed by no significant trend after the hunting ban was introduced (Loch Lomond) or no significant trend either before or after 1982/83 (Loch Ken). Furthermore, in southwest Scotland, the wintering flock at Stranraer showed a significant increase before *and* after 1982, but the rate of increase declined after protection; moreover,

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116. A typical first-winter family party of Greenland White-fronted Geese *Anser albifrons flavirostris* gathering for a drinking bout at Wexford North Slob, Ireland. Note the more conspicuous white facial 'frons' and black belly-bars of the two adult parent birds to either side, compared with the more restricted frons and lack of pronounced belly-barring on the five first-winter birds in the centre of the group.

as at Wexford Slobs, numbers at Stranraer apparently started to decline from as early as the late 1980s (fig. 7). Clearly, factors other than hunting mortality were affecting winter population levels at a local scale, although at those sites where shooting pressure was heaviest (Wexford, Islay and Kintyre), the hunting moratorium had an immediate effect on local numbers.

Population growth in the 1980s–90s and variation among sites

We are now confident that Greenland White-fronted Geese wintered regularly at some 80 sites in Britain & Ireland in the early 1980s (fig. 2). However, even during the period of increase (at an average rate of c. 5% per annum for the population as a whole; Fox *et al.* 1998b), numbers at different sites showed different trends. At the peak period of overall increase, in the mid 1990s, 20 sites showed a significant rise in wintering numbers after protection, 35 showed no significant trend, 18 showed a significant decrease, and flocks at seven sites had disappeared since 1982 (Fox *et al.* 1998b). At that time, local factors seemed to affect the propensity of a wintering flock to increase or decrease. Studies in Ireland revealed that flocks experi-

encing low disturbance from human activities (e.g. agriculture or recreation) and with many alternative feeding areas generally showed higher rates of increase than those using a restricted number of sites where disturbance rates were high (Norriss & Wilson 1988, 1993). However, because individuals show high levels of site loyalty (Wilson *et al.* 1991), there is limited potential for recolonisation of deserted sites, or for large-scale immigration from other areas to supplement declining flocks. Only two apparently new sites have been 'colonised' as winter resorts by Greenland White-fronted Geese since 1982 (Sullom Voe, Shetland, and Stabannan, Co. Louth); interestingly, neither of these flocks has persisted after the late 1990s. There are also consistent records of small numbers wintering in Rogaland, southern Norway. This is therefore a classic metapopulation, where wintering numbers at various sites show different trends in abundance that contribute to an overall pattern in global numbers.

Because of the long-established conservation interest associated with this population, there are extensive data from ringing recoveries, resightings of marked individuals and satellite telemetry. Marking schemes using leg rings or

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neck-collars show that very few individuals are seen at more than one wintering site within a season, and most examples involve geese reported briefly at staging points within the non-breeding range en route to their main winter quarters (Warren *et al.* 1992b). The same site-loyalty generally holds between winters, and site-interchange of marked Greenland White-fronted Geese is relatively unusual; most adult birds return to the same fields on the same farms, winter after winter. Nonetheless, 14% of all marked birds seen in consecutive winters changed site, mostly after (re-)pairing, when one member of a newly formed pair-bond is likely to have to change wintering site (Warren *et al.* 1992b). Results show that

birds in the south of the wintering range tend to breed in the north of the breeding range, while those wintering in the north (Scotland) nest in the southern part of west Greenland – a classic 'leapfrog' migration pattern (Salomonsen 1950; Boyd 1958; Fox *et al.* 1983; Kampp *et al.* 1988; Fox *et al.* 2003). Non-breeders caught together during moult in Greenland disperse throughout the wintering grounds, so birds associating in winter may not constitute stable groups maintained at other stages of the annual cycle. Family relationships are exceptionally strong in the Greenland White-fronted Goose, however, unusually so among wild geese (Warren *et al.* 1993 and unpubl. data). Family bonds persist during spring and autumn migration in Iceland (Fox *et al.* 2002) and on the breeding grounds, where non-breeding associates assist with vigilance and nest defence against predators (Stroud 1981; Fox *et al.* 1995).

During the mid 1990s, the conservation status of the Greenland White-fronted Goose seemed favourable. The flyway conservation manage-



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117. Kentra Moss in Argyll, an outstanding example of an oceanic raised bog system showing the pronounced pool-and-hummock structure so attractive to feeding Greenland White-fronted Geese *Anser albifrons flavirostris*. The birds traditionally forage on the below-ground parts of Common Cottongrass *Eriophorum angustifolium* and White Beak-sedge *Rhynchospora alba*, which thrive in the wet *Sphagnum* moss-filled hollows of such landscapes.

ment plan (Stroud 1992), drafted with the support of the National Parks and Wildlife Service of the Republic of Ireland and Wetlands International (although never ratified by the Range States), had made maintenance of range and status throughout the wintering range a priority objective. Even during this period of most rapid population expansion, however, the decline and disappearance of some local flocks hinted at challenges to meeting such targets (Fox *et al.* 1998b).



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118. Greenland White-fronted Geese *Anser albifrons flavirostris* foraging on Kentra Moss, Argyll. Bog-feeding geese can remain well hidden and are often extremely difficult to find in this habitat.

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The long-term decline in breeding success

At the same time as the global population of the Greenland White-front was expanding, a more subtle change was becoming apparent, one which was to affect all wintering flocks, most conspicuously at the major aggregations at Wexford Slobs and on Islay. At Wexford, numbers peaked in the early 1990s and began to decline thereafter, although numbers have stabilised and shown some recovery since 2000 (fig. 3). The local causes were not immediately apparent, as the site was managed sympathetically for wintering geese. Although there was no significant trend in the proportion of young recorded in sample counts of autumn flocks prior to the hunting ban, a long-term decline in this measure gradually became apparent after 1982 (fig. 8). Over the same period, resightings of marked individuals enabled age- and year-specific survival rates to be estimated using capture-recapture techniques (Burnham 1993) and the multi-stage models of Hestbeck *et al.* (1991). These analyses showed that there had been no significant change in annual adult survival or emigration from Wexford over the period (Fox 2003). In relatively long-lived birds such as geese, overall population abundance is more sensitive to small changes in annual survival than it is to relatively larger changes in reproductive success (Tombre *et al.* 1997; Pet-

tifor *et al.* 1999). The discovery that the decline in abundance at Wexford was the result of a long-term decrease in the production of young, and not of falling survival, was unexpected.

The proportion of each year-class of goslings captured and marked in their first winter at Wexford and which survived to breed *at all* during their lifetime has fallen since marking began, from c. 15% in 1983 to less than 5% in the early 1990s (Fox 2003). This is an extraordinary statistic (assuming that marked birds are representative of the population as a whole), which suggests that, even in the population's heyday, 85% of Wexford Greenland White-fronted Geese *never* bred successfully during their lifetime. This highlights the important distinction between 'actual' and 'effective' population size (the latter being the number of birds that do in fact contribute offspring to the next generation). The question of whether marked birds are truly representative of the population as a whole is extremely difficult to answer, but there are indications that collared birds had larger brood sizes and greater reproductive success than unmarked birds, probably because baiting for cannon-net catches attracted behaviourally dominant individuals and family groups (i.e. already successful breeders; S. M. Warren unpubl.). Among the same sample of neck-collared cohorts, there was also an

increase in the mean age of first breeding, from 3.5 years among goslings hatched before 1988 to c. 5 years in subsequent years (Fox 2003). Because the species is so long-lived and shows delayed recruitment, it is not possible to compile these statistics on more recent cohorts. Nevertheless, following the hunting ban, geese were breeding successfully progressively later, and as time went on, fewer and fewer individuals were breeding successfully at all in their lifetime. It thus appears that some mechanism was, and apparently still is, operating that increasingly precludes young geese from becoming successful breeders.

Clearly, a decline in the proportion of birds breeding successfully may not be a problem in an expanding population, espe-

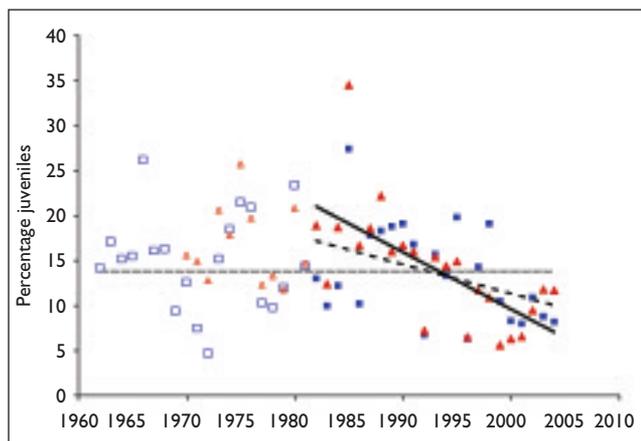


Fig. 8. Long-term changes in the proportions of young Greenland White-fronted Geese *Anser albifrons flavirostris* sampled in winter from Wexford Slobs and Islay (data courtesy Parks and Wildlife Service Ireland and GWGS/Dr Malcolm Ogilvie, respectively). Open symbols indicate values prior to protection from winter hunting in Scotland and Ireland, solid symbols post-protection. Squares represent data from Wexford, triangles those from Islay. The horizontal dotted line indicates the overall mean value; the solid line the significant decline at Wexford since protection; and the sloping dotted line the regression model for Islay, which is almost statistically significant.

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119. Many Scottish Hebridean Greenland White-fronted Goose *Anser albifrons flavirostris* flocks are associated with low-intensity pastoral agriculture, which represents such an important landscape for a variety of nature conservation interests. This photograph shows a typical flock exploiting rushy, unimproved pastures near Loch Assapol on Mull.

cially while, in absolute terms, more birds are reproducing. Ultimately, however, if the absolute production of young in any one year at a site fails to balance the losses from (i) death and (ii) the difference between emigration and immigration, local numbers will decline. This was the case at Wexford after the early 1990s (but perhaps not since 2000; fig. 3). By the late 1990s, the same pattern was becoming evident at other sites as well, with a gradual slowing in the rate of increase among many winter flocks. Although not immediately obvious, the produc-

tion of young by birds wintering on Islay has also declined, until overall numbers began to fall there too in the early part of the twenty-first century. This phenomenon now seems widespread among the wintering flocks and, as a result, the population as a whole is now in decline.

So what are the causes of this most recent downturn in fortunes, and, in particular, why is breeding success declining? Greenland White-fronted Geese are protected from hunting on the wintering grounds and benefit from the



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120. Many wintering flocks of Greenland White-fronted Geese *Anser albifrons flavirostris* are still heavily reliant upon natural wetland and seasonally inundated areas, especially as overnight roost sites. The Loons RSPB reserve, Orkney, is one such site which also remains an important feeding area, despite use of adjacent farmland for alternative feeding areas.

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provision of wildfowl reserves, positive management and site safeguard, particularly of roosts. Large areas of the breeding grounds are protected and the spring shoot was closed in Greenland in the 1980s (Stroud 1992). It is likely that several varied, interacting and often conflicting factors could potentially contribute to the lowering of reproductive success (and ultimately numbers) of the geese, and these are considered below.

Potential causes for the decline in breeding success

Density dependence

Perhaps the most plausible explanation is that the increase in overall numbers of Greenland White-fronted Geese since the early 1980s has inhibited reproduction in some way. Perhaps higher densities on the breeding areas filled the available capacity of the environment to support their reproductive output at previous levels. Food limitation might be one obvious constraint (see Box 1), such that competition among individuals (i.e. intraspecific competition) now limits the number of breeding pairs and/or their capacity to produce and raise young.

Trinder *et al.* (2005) showed some evidence for density-dependent regulation on Islay but,

using winter numbers as a proxy measure of density, there was no statistically significant relationship between the numbers of geese in any one year and the percentage of young returning the next since hunting protection was conferred, either at Wexford Slobs or on Islay. The same analysis showed no significant effect using global population size (the estimated total population) versus the production of young by birds wintering on Islay, although there was a significant result for the Wexford population. These conflicting results do not prove whether local density-dependent effects exist or not, but this uncertainty strongly suggests that the increase in the overall abundance of the population is not the only reason that reproductive success has fallen. Since 2002, numbers of the population as a whole have continued to fall sharply; this should mean that density-dependent regulation would be relaxed and breeding success would begin to recover. Yet there is no evidence for such a recovery; on the contrary, the percentage of young returning to the winter quarters has continued to fall. Consequently, while density is likely to play some role in the regulation of breeding, it seems unlikely to be the whole explanation.

Feeding ecology

Box 1. 'Capital' versus 'income' breeders

Recent studies suggest that Arctic-nesting geese adopt a mixed 'capital/income' breeding strategy. They produce eggs that are derived from nutrients obtained from both food ingested on the breeding areas ('income') and resources they have brought with them, accumulated at least on the staging areas and possibly from the winter quarters ('capital'). By measuring the ratio of different stable isotopes of specific elements present in the eggs, it is possible to show from what source the female obtained vital nutrients that she later invested in formation of her clutch. This is because of distinctive geographical patterns in stable isotope ratios or those present in specific food items consumed at key stages in the annual cycle (Gauthier *et al.* 2003). We also know that female geese undergo rapid follicle development (when many of the key nutrient stores are laid down in the developing egg follicles) well in advance of laying the first egg. Based on dissection of shot birds and the satellite-tracking of individual geese, we know that many geese start this process on staging areas, well before arrival in the breeding areas. In the case of Svalbard Pink-footed Geese *Anser brachyrhynchus*, this occurs on Norwegian staging areas before their final ocean crossing to nesting areas in Svalbard (Glahder *et al.* in press). This has also been demonstrated for Greenland White-fronted Geese, since a female was recently shot in spring on migration in east Greenland (en route to the nesting grounds) with well-developed follicles in the ovarian ducts (J. Nyeland *in litt.*). This female had thus already invested nutrients in the egg bodies developing in the oviducts as a basis for her clutch by using the nutrients derived during her period of staging in Iceland, potentially supplemented with resources brought from the wintering quarters. Food limitation affecting reproductive success may therefore not be confined to the breeding areas, but could potentially occur at any stage during the late winter or on spring staging areas.

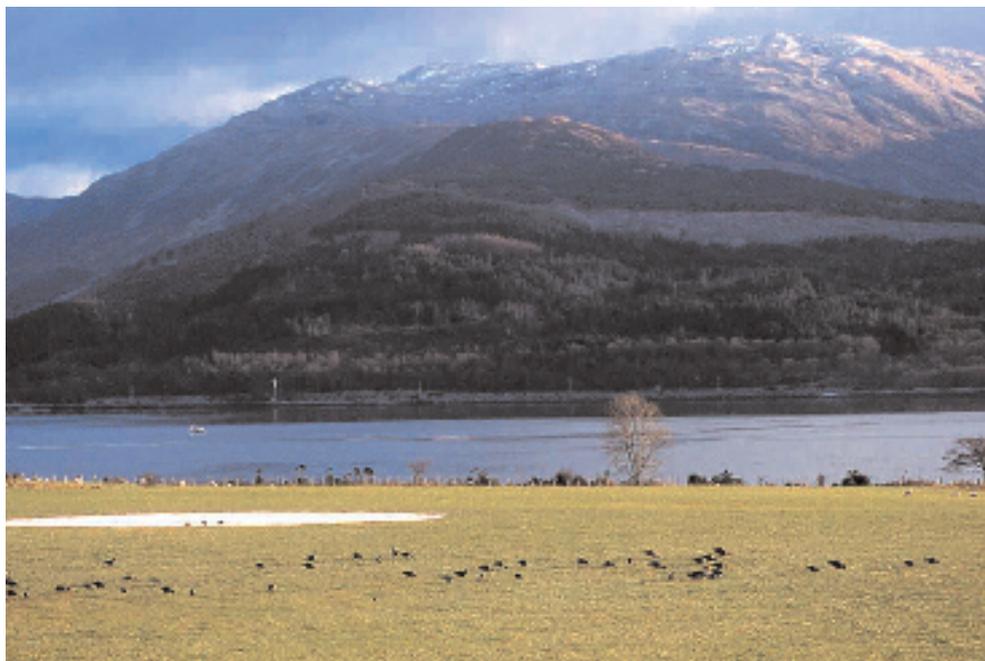
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Recent studies of Black-tailed Godwits *Limosa limosa* in the UK have shown that birds on the wintering grounds have 'filled up' the best habitat first. This means that, with further increases in the population, birds are displaced to poorer quality habitat, which is associated with reduced survival and reproductive success (Gill *et al.* 2001). One conspicuous feature of winter habitat use of Greenland White-fronted Geese in recent years has been the declining use of their traditional winter domain – peatland and bog habitat. Their use of this habitat may well explain the Greenland White-front's restricted distribution since, in former times, they were confined to oceanic patterned (quaking) mires along the western fringe of Europe, where traditional food items were abundant. These were predominantly the lower stems of the Common Cottongrass *Eriophorum angustifolium* and overwintering bulbils of White Beak-sedge *Rhynchospora alba* (Ruttledge 1929; Cadman 1953, 1956, 1957; Pollard & Walters-Davies 1968; Fox *et al.* 1990). These food items are extracted from below ground level, in bog pools and floating *Sphagnum* moss lawns. The high rainfall necessary for the formation of such mires and open pool systems is confined to Britain, Ireland, Iceland and Scandinavia, but north of Britain & Ireland these

ecosystems are frozen in winter, precluding extraction of below-ground plant parts, and are thus effectively denied to the geese as winter foraging habitat. Consequently, prior to human agriculture, Greenland White-fronts were probably confined to natural wetlands in Ireland and western Britain in winter.

Since the early twentieth century, Greenland White-fronted Geese have foraged increasingly on agricultural habitats (Ruttledge & Ogilvie 1979; Mayes 1991; Fox *et al.* 2005). In the 1950s, almost half the known wintering flocks used peatlands (often as daytime feeding areas), but less than 20% do so now, and mostly as night-time roosts rather than as primary feeding sites. Increasingly, the population exploits spilled grain in autumn and early winter and moves to intensively managed, reseeded grassland for most of the winter, supplemented (where available) by root crops in midwinter, when grass growth rate slows. Many flocks still exploit rushy pasture and low-intensity grassland, but the trend has increasingly been to shift to more intensively managed, high-energy, agricultural habitats and away from natural wetlands and low-intensity farmland.

The 'junk food' hypothesis therefore states that Greenland White-fronted Geese have been able to increase their rate of food intake and



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121. Greenland White-fronted Geese *Anser albifrons flavirostris* at Ardnachlach, Lorn, Argyll. In Lorn, the geese use a network of small improved and semi-improved fields around Loch Creran, flying between them when disturbed.

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exploit high-energy food-plants by shifting to farmland habitats on the winter quarters; but that these benefits are offset by some cost to body condition which has influenced breeding success. It might, for example, reflect a lack of critical nutrients (rather than energy), which are less abundant in agricultural crops and grasses than in more natural food-plants (Reed 1976). If this was the case, we would expect that flocks exploiting natural peatland habitats in winter would produce more young than those on farmland. In fact, the opposite is the case – flocks wintering on intensive farmland produced, on average, 10% more young each year than those feeding almost exclusively on peatland habitats (Fox *et al.* 2005). Furthermore, since flocks using farmland were far larger than those using peatlands, they produced substantially more young in absolute terms. As a result, flocks on the best agricultural land in the 1990s (such as those on Islay and Kintyre) were those showing the most rapid increases and flocks on less intensive agricultural areas were declining or stable (Fox *et al.* 2005). In contrast, even during the period of increase in the 1980s and 1990s, the small flocks associated with bogland habitats in Ireland were those showing declines.

Consequently, birds exploiting the artificial habitats of our farmland landscape comprise an increasing proportion of the total population, now far exceeding those using natural habitats.

The consequences of these patterns are not clear, especially since we know that birds wintering together do not necessarily associate on the breeding areas. It may be that birds leaving the winter quarters in good condition after feeding on rich agricultural habitats are more likely to select high-quality staging areas in Iceland and Greenland. It may also be the case that their good condition gives them a competitive advantage in agonistic interactions at spring staging areas, where good foraging habitat is known to be highly limited in time and space (e.g. on arrival in Greenland; Glahder 1999; Glahder *et al.* 2002). In contrast, a goose exploiting low-quality winter habitat, departing in poor condition in spring, will probably fail to displace fitter individuals from the best spring-foraging opportunities en route to breeding areas. Such an individual is therefore likely to perform less well during the breeding period than a goose that fed well during the winter. In this way, conditions experienced on the wintering grounds may further affect foraging



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122. Increasingly, Greenland White-fronted Geese *Anser albifrons flavirostris* have adapted to more intensively managed grasslands throughout their winter range. This example is from Big Isle, Lough Swilly in Co. Donegal, the fields in this photograph holding almost 600 feeding Greenland White-fronted Geese when the picture was taken.

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opportunities of an individual throughout the annual cycle and hence affect its overall fitness, in terms of reproductive potential and perhaps even survival.

A similar shift in feeding habitats has been witnessed in Iceland, where Greenland White-fronts stage on spring and autumn migration (Francis & Fox 1987; Fox *et al.* 1999, 2003). Here, geese traditionally fed on wetland habitats during both migration periods. They exploited the lower stem-bases of Common Cottongrass and the morphologically similar Lyngby's Sedge *Carex lyngbyei* that grows in dense stands in base-rich lowland fen habitats, including old wet sedge hay meadows (Francis & Fox 1987). In recent years, however, the geese have switched increasingly to grazing on drained dry grassland hayfields. These are either dominated by the native grass species Tufted Hair-grass *Deschampsia cespitosa* and Smooth Meadow-grass *Poa pratensis*, or have been reseeded with an introduced Norwegian-bred strain of Timothy *Phleum pratense* (Fox *et al.* 1998a; Kristiansen *et al.* 1998, 2000). Greater densities of geese occur on reseeded *Phleum* hayfields, where they can maintain higher intake rates of better-quality food than on fields with native grasses (Fox 2003; Nyegaard *et al.* 2001) and it seems likely that all hayfields offer geese more profitable feeding opportunities than natural wetlands. It is not entirely clear over what

period this change in use of staging habitats occurred, but land-use changes have been most rapid since the 1960s. Because it is difficult to separate these effects from other changes throughout the annual cycle, it is impossible to comprehend fully the consequences of this major shift in habitat use. Nonetheless, the provision of readily available, high-quality, grassland forage, where geese can sustain much higher intake rates of energy than from natural wetlands, is unlikely to have been the major cause of recent declines in reproductive success.

Effects of global climate change on the breeding areas

Zöckler & Lysenko (2000) showed that there was a correlation between mean June temperatures in west Greenland and the production of young, as sampled on the wintering grounds at Wexford Slobs in the following autumn, raising the possibility that a cooling climate in west Greenland has reduced the reproductive potential of the geese. Global climate change models have been predicting a cooling of the climate in the northeast Canadian Arctic, Baffin Island and parts of northwest Greenland and there is evidence of this from Greenland (Rigor *et al.* 2000). However, during 1974–2002, there had been no significant trend in the May and June temperatures from Kangerlussuaq (66°59'N 50°37'W, in central west Greenland) or Ilulissat



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123. Traditionally, Greenland White-fronted Geese *Anser albifrons flavirostris* fed on Common Cottongrass *Eriophorum angustifolium* and Lyngby's Sedge *Carex lyngbyei* during their staging period in Iceland. The sedge resembles Common Cottongrass in morphology and the below-ground low-stem storage organs are highly nutritious. The plant occurs nowhere in Europe outside Iceland, but can occur in great abundance in dense stands, as seen here at Hvanneyri, in western Iceland.

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(69°13'N 51°05'W, farther north in the breeding range), where Scottish and Irish birds, respectively, are thought to summer. Moreover, attempts to model four different reproduction measures (overall percentage of young, number of families, proportion of potential breeding pairs returning with young and production of young per potential breeding female) using average May and June temperatures for a longer time series from Kangerlussuaq and Ilulissat were largely unsuccessful. Of all the models, only those predicting the overall percentage of young and the number of families on Islay, based on mean temperatures in Kangerlussuaq in the preceding June, produced significant results. It would, therefore, seem that although summer temperatures on the breeding grounds do have some effect on the success of birds attempting to reproduce under some circum-

stances, there is no evidence for any strong wider effect of climate as an explanation for the overall decline in reproductive output.

Canada Geese on the breeding areas

One poorly studied consequence of recent expansions (and consequent temporal and spatial overlap) in the number and distribution of northern-nesting geese is the degree to which interspecific interactions, such as competition for food, may occur. After all, all northern geese are essentially herbivores with the same body plan (Box 2).

Where these interactions are unequal in nature, effects on local goose distribution and abundance may have an impact at the population level, because competition from a dominant species may affect access to the best feeding opportunities, reduce body condition

Box 2. Goose feeding ecology, the benefits of modern agriculture and the potential for competition

In order to minimise their weight in flight, geese have evolved a relatively simple digestive system. Unlike ruminants, they have no heavy rumen and digestive apparatus to assist with digestion of the more fibrous element of their food (sheep do not fly for good reasons!). Instead, geese rely upon a rapid and continuous throughput of plant food, which is digested less efficiently. Wild geese therefore need to maintain a sustained throughput of relatively low-quality food, from which they can rapidly extract the available soluble fraction. To do this, they typically feed by selecting the best-quality plant parts. These include storage organs where plants have accumulated protein, fat and carbohydrate for future growth (such as seeds, tubers and rhizomes) or, as in the case of grazing, the growing tips of young leaves, which typically are high in protein but low in fibre compared with most plant material. In the relatively short season and harsh conditions of the Arctic, these sources of food may be highly limited, so the likelihood for competition is potentially greater.

In contrast to most birds associated with agricultural habitats in the last 30 years, geese have increased in numbers spectacularly in the northern hemisphere. In response to the spilled grain of the autumn harvest, the plethora of root crops and especially increasing areas of farmland devoted to the production of highly digestible, specially bred, protein-rich grasses, most geese have flourished and their numbers have expanded through enhanced annual survival and breeding success. Because farmland has largely been claimed from formerly afforested areas, it seems fair to assume that there are now very many more geese on the planet than in recent millennia. While such a surfeit of food may be sufficient to avoid any limitation of numbers in the winter quarters, their Arctic breeding grounds have not changed substantially in either area or quality. As numbers of different populations have increased, so have their breeding ranges. Several species have shown dramatic extensions to their nesting grounds; in the case of the Barnacle Goose *Branta leucopsis* (formerly restricted to the Russian high Arctic), this has included colonisation of islands in the Baltic Sea, latterly spreading to nest in The Netherlands in areas where they formerly wintered only. Species that were formerly allopatric, i.e. nesting in separate geographical areas, are increasingly showing sympatry as their breeding ranges overlap. Where geese feed on completely different food items and show no aggression towards each other, this meeting is likely to have no effect on the population dynamics of either species. But where there are limits to the amount of food and the two species first encountering each other select for similar dietary items, the potential for competition for these food resources is high and interactions are likely to occur.

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and ultimately reduce breeding success or survival in the weaker species. This may occur where the subordinate species loses access to favoured feeding areas because of the aggressive nature (or numerical superiority) of the dominant species. There are certainly strong indications of behavioural and other interactions between Greenland White-fronted Geese and Greater Canada Geese *Branta canadensis*, which have colonised west Greenland in recent years. Almost all populations of Canada Geese in North America have shown increases in numbers across the continent, largely as a result of unlimited winter-feeding opportunities created by intensive agriculture. The population of Greater Canada Geese *B. c. interior* nesting in northern Quebec and wintering in the eastern USA has also benefited from several years of partial protection from hunting there in the 1990s. This population has spread to west Greenland since the 1980s (confirmed by satellite telemetry, ringing recoveries and resightings, and DNA analysis; Fox *et al.* 1996; Kristiansen *et al.* 1999; Scribner *et al.* 2003). During wing moult, Greenland White-fronted Geese were observed to feed more on low-quality moss species and to show lower food-intake rates where they mixed with Canada Geese than where they foraged alone. Canada Geese were also seen to be behaviourally dominant over Greenland White-fronts in all observed encounters, regardless of relative abundance (Kristiansen & Jarrett 2002).

Since the late 1980s, in one regularly surveyed area, Canada Geese have displaced the endemic Greenland White-fronted Goose from territories where it was formerly the only goose species present (Kristiansen & Jarrett 2002). Aerial surveys of extensive areas showed that, despite favouring the same geographic region, the two species were less likely to occur together than by chance, suggesting some segregation at a local scale (Malecki *et al.* 2000). Repeat surveys of breeding areas in 2003 confirmed the continuing and extensive loss of former breeding territory to the colonist species (J. Madsen unpubl.), so a major resurvey

was undertaken in June 2005. Although the final results of that survey have yet to be analysed, first indications suggest that the overall density of nesting Canada Goose pairs did not change between 1999 and 2005, but the number of breeding Greenland White-fronts was one-third of those recorded in 1999. What was striking, however, was the six-fold increase in overall numbers of Canada Geese on the survey between 1999 and 2005 compared with a halving in the overall abundance of Greenland White-fronts. Changes in the numbers of breeding White-front pairs detected on the breeding areas corresponded well to the relative changes in the numbers of families returning to the winter quarters. Furthermore, the reduction in overall numbers between the aerial surveys mirrored the global population trend in that time; hence we have some confidence that the survey results reflect what is happening on the ground.

Based on the survey areas sampled in 2005, the Greenland White-fronted Goose is still twice as abundant as the Canada Goose in west Greenland. Furthermore, the six-fold increase in Canada Geese and the halving of Greenland White-front numbers remains only a correlation. Just because Canada Geese have increased while White-fronts have declined does not provide direct evidence for cause and effect. However, the distributions of both species differed greatly in the two surveys. Both species were more common in the south of the range in 1999, when the spring thaw was delayed, compared with an 'average' season, but both were



124. Many Icelandic wetlands were drained in the twentieth century, resulting in lowering of the water table and loss of habitat in the southern and western lowlands of Iceland used by Greenland White-fronted Geese *Anser albifrons flavirostris* during spring and autumn. Here, drainage of wetlands can be seen near Hvanneyri, in western Iceland.

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more common in the north of the same surveyed range in 2005, when snow cover was more typical. This suggests that both species tend to settle in response to snow patterns, but favour the same geographical range despite large differences between years in the spring thaw. Furthermore, in both years, there was strong evidence that, at the local level, the two species were segregated. Canadas and Greenland White-fronts occurred together along the transects flown less often than would be expected by chance. Hence, despite the general selection for the same geographical areas, the two species seemed to avoid each other at a local level. There does, therefore, seem to be some circumstantial evidence to suggest that the spectacular increase in Canada Geese in west Greenland may have been exerting some effect on the local distribution of Greenland White-fronts, which in turn may be affecting the reproductive output of the latter. More detailed field studies are needed throughout the summer so that we can understand more about interactions between the two species, although the probabilities of finding the two species in sympatry to study are becoming increasingly infrequent.

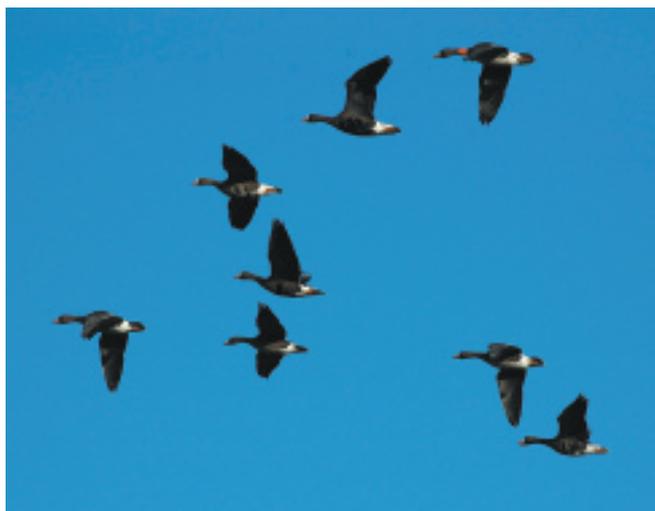
Conclusions

Finding answers to relatively simple questions regarding Greenland White-fronted Geese and their population change has proved difficult, in

part because the potential causes for changes in their abundance are spread along a migration corridor from the northwest corner of Greenland to the southeast corner of Ireland. It is not possible to undertake a controlled laboratory experiment to establish simple cause and effect, so we need to rely on a combination of long-term observations and modelling, and must hope to unravel the potential causes by a process of elimination. The key element in understanding the processes that affect the population's conservation status has to be the long-term international co-operation invested in survey, monitoring and research. It is becoming increasingly important to obtain reliable basic demographic monitoring data (i.e. in addition to just head-counts of abundance) if we are to be effective in targeting scarce resources into conservation effort.

In the case of the Greenland White-fronted Goose, our knowledge of reproductive patterns, hunting bags and survival has enabled some assessment of the additive effect of hunting mortality that justifies manipulation of the kill as an effective management tool for this population. Modelling has identified falling reproductive success as the long-term cause of the decline in numbers, despite the fact that modelling also shows that a relatively long-lived bird such as this is more susceptible to changes in adult survival than to changes in breeding success. Individual marking shows that an

increasing proportion of young birds are failing to reproduce, while those that do breed start later in life, adding to the overall downturn in abundance. In this way, we can be quite certain that the cause of the decline is falling reproductive success owing to fewer birds of breeding age reproducing successfully, even though we cannot precisely identify the factor(s) involved. There is no evidence to suggest an increase in nest predators on the breeding grounds. It does seem likely that greater numbers of White-fronts may have had a contributory (density-dependent) effect, just as lower June temperatures seem to have some effect on



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125. A family party of eight Greenland White-fronted Geese *Anser albifrons flavirostris* in flight. The collar bears the insignia PIH, and is borne by a gosling caught and marked at Hvanneyri, western Iceland, in October 2004; the bird is seen here on 15th October with its five unringed siblings and two parents, at Hvanneyri.

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some birds. The true cause of the decline is yet to be established with certainty, yet perhaps the single most important factor, looking at the current evidence, is likely to be the negative interactions with Canada Geese which they increasingly encounter on the breeding grounds.

Management implications – just what can be done?

The apparent robustness of the Greenland White-fronted Goose to adapt to novel feeding opportunities presented by the rapid changes in modern agriculture has enabled it to adjust to major changes in extent and quality of its natural habitat since 1940. It may well be that human activities have modified and fragmented its traditional peatland wintering habitats to the extent that they no longer provide adequate energy and nutrients. There is, however, no doubt that those flocks that have shifted to modern agricultural landscapes have, since the early 1980s, produced more young than those which continue to winter on more traditional bogland habitats and low-intensity agriculture. It is ironic that changes to goose management in part of another continent – the eastern USA – have encouraged the expansion in numbers of Greater Canada Geese that seems to have led to that species' colonisation of west Greenland. This extension of range may now have affected the reproductive success and population size of a similar goose species wintering far away on the western fringe of Europe.

But what can be done to stabilise the population of Greenland White-fronted Geese and maintain the current distribution and abundance of this race? If the Canada Goose *is* the problem, there is little that we in Europe can do to modify the numbers of a population that is known to winter along the Atlantic coast of North America. In Greenland, the hunting laws are designed to protect newly colonising species, but the Greenland Home Rule Authority declared the Canada Goose a huntable species there in 2004. However, geese are generally not a favoured quarry in Greenland because their dis-

persed nature makes them extremely difficult to kill in any number. Their arrival in spring is one of the few periods when birds are highly concentrated, at early thawing spring staging areas (Glahder 1999; Glahder *et al.* 2002). This coincides with snow melt and the break-up of sea ice, however, making human movements away from settlements generally difficult, although areas accessible on foot may still be heavily exploited. During moult, when they are flightless, geese are extremely wary and resort to the safety of water in relatively small groups, where they are difficult to catch. In late summer, we know little about their distribution and abundance but Inuit hunters in inland west Greenland (where the geese occur in greatest numbers at this time) continue to target Caribou *Rangifer tarandus* and Arctic Char *Salvelinus alpinus*, as they have done for over a century (Müller 1906), which suggests that these are preferred or easier prey than geese.

Satellite telemetry and collar-marking studies show that Canada Geese from Greenland have a distinctive migration route and timing (Kristiansen *et al.* 1999; Schribner *et al.* 2003). In north and east North America, however, as soon as they mix with large numbers of birds that gather from breeding areas in Labrador, Newfoundland, northern Quebec and Baffin Island, there is nothing to distinguish them from geese of other breeding areas. Consequently, there seems no opportunity to target the hunt on Canada Geese from Greenland on non-breeding areas in North America to reduce numbers and potentially



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126. JSU, a collared Greenland White-fronted Goose *Anser albifrons flavirostris*, photographed in flight with its unringed mate at Wexford Slobs, Ireland.

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alleviate pressure on White-fronts. Perhaps we should just hope that the two species find an eventual means of coexisting in west Greenland by avoiding foraging on the same food items in similar habitats, just as they do throughout vast areas of the central Canadian Arctic (e.g. Carriere *et al.* 1999).

Greenland White-fronts remain protected throughout the majority of the wintering grounds and more or less all internationally important sites enjoy some level of site safeguard or positive management, even if some have not yet been formally designated as Ramsar sites and/or SPAs. Bag returns suggest that few Greenland White-fronted Geese are shot in Greenland, and illegal shooting is thought to be extremely low. The population continues to be hunted in Iceland in the autumn, however, where at least 3,000 per annum have been shot in recent years. It is important to emphasise that the autumn hunt in Iceland was sustained for many years in the 1980s and 1990s when the population was maintaining a steady rate of annual increase in excess of 5%. At that time, such a kill was sustainable, in the sense that it was not enough to halt the increase in numbers (even though it undoubtedly restricted the rate of increase below its full potential). Unfortunately, there were no hunting statistics gathered during the 1980s and early 1990s, but since 1995 the Icelandic Wildlife Management Institute has collated annual bag records, which show an increase in numbers killed, from 2,947 in 1996 to 3,685 in 2001, the last year for which data have been published. Because of population declines over that period, the numbers shot represented 8% of the autumn flight in 1996, but this had risen to 12% by 2001. We can only guess at the trend in the kill since that time and its effect in the face of the continued decline in total population size. It is clear, however, that the kill in Iceland at the 2001 level was approaching the total annual mortality of earlier years and if this continues at the present rate, the inevitable decrease in annual survival will further exacerbate the rate of overall population decline. While the hunting kill in Iceland was not the cause of the Greenland White-front's long-term decline, there is no doubt that a moratorium on hunting there now would substantially reduce the rate of decline, since this level of hunting is demonstrably unsustainable under present conditions.

It is frustrating that the pioneering initiative to gather the Range States involved in the conservation of the Greenland White-fronted Goose at the Wexford workshop on 4th–6th March 1992 failed to result in the formal agreement of the draft plan (Stroud 1992). The adoption of such a plan would have secured agreement on alert limits and triggered action in response to the present declines at a far earlier stage than we have reached today. As it is, after many years of sustained conservation effort, we now see the population returning rapidly to pre-protection levels of the late 1970s, with little sign of responsive conservation actions despite the possibility to do so. On a more positive note, great strides have been made through the development of a national policy framework for goose management in Scotland (Finnie & Brankin 2005). Scottish Natural Heritage has recently (March 2006) launched its Species Framework Initiative, listing the Greenland White-fronted Goose as a priority population in Scotland, one requiring urgent direct management actions to increase its range and population size. SNH is inviting written responses to its consultation paper before 30th June 2006 to concentrate and co-ordinate actions (see <http://www.snh.org.uk/strategy/sr-pc00.asp>). Part of these actions will necessitate research on the breeding grounds to determine whether interactions with Greater Canada Geese during the pre-breeding and breeding periods may be responsible for the observed population trends in the Greenland White-front. At present, there are moves afoot by concerned NGOs in Iceland to promote voluntary initiatives that could reduce the hunting kill, and such initiatives should be wholeheartedly welcomed. There may, however, be scope under the African-Eurasian Waterbird Agreement to encourage internationally collaborative conservation actions for the population (Appendix 1).

The case of the Greenland White-fronted Goose may offer a worthwhile lesson on the need for international collaboration, not just in research and conservation (which has shown considerable success) but also in co-ordinating international conservation actions. This may also offer useful perspectives on the flyway conservation needs for other waterbirds. As long as hunted waterbird populations continue to show stable or increasing trends, complacency about their management is a low-risk strategy, but

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once in decline, the restoration of populations to favourable conservation status offers different and interesting challenges. The moral is that conservation needs to be responsive; remedial actions should be taken early – patients are typically easier (and cheaper) to treat before they reach the intensive care ward!

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Dr A. D. (Tony) Fox, Department of Wildlife Ecology and Biodiversity, National Environmental Research Institute, Kalø, Grenåvej 12, DK-8410 Rønne, Denmark

David Stroud, Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough PE1 1JY

Alyn Walsh, National Parks and Wildlife Service, Wexford Wildfowl Reserve, North Slob, Wexford, Ireland

John Wilson and David Norriss, National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, 7 Ely Place, Dublin 2, Ireland

Ian Francis, RSPB Scotland, 10 Albyn Terrace, Aberdeen AB1 1YP



Appendix I. Opportunities for international co-operation

African-Eurasian Migratory Waterbirds Agreement

The Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) is an international conservation treaty that came into force in 1999, currently (April 2006) ratified by 53 Contracting Parties, including the EU, the UK and the Republic of Ireland; Iceland and Greenland have yet to ratify AEWA.

Governments adopting AEWA formally recognise 'the need to take immediate action to stop the decline of migratory waterbird species' and commit to undertake a range of actions to this end both nationally and collaboratively with other countries. These actions include research and monitoring, and the development of species action plans (http://www.unep-awea.org/documents/agreement_text/action-plan-overview.htm).

The legal requirements of AEWA for species in its highest status category, which includes the Greenland White-fronted Goose, specify that: 'hunting may continue on a sustainable use basis where hunting of such populations is a long-established cultural practice. This sustainable use shall be conducted within the framework of special provisions of a species action plan at the appropriate international level.'

Notwithstanding the fact that Iceland and Greenland have yet to ratify the agreement, AEWA gives the UK and Irish Governments a mechanism to take forward necessary conservation actions with Iceland and Greenland to restore Greenland White-fronted Geese to favourable conservation status. Indeed, the UK Government's Implementation Plan for AEWA (Defra 2002a) 'aim[ed] to conclude agreement on Greenland White-fronted Goose international plan in 2002/03', while the UK's implementation of the Ramsar Convention's Strategic Plan (Defra 2002b) stated that the UK would 'Finalise Memorandum of Understanding with Iceland, Greenland and Ireland concerning the common conservation management of Greenland White-fronted Geese by 2004, stressing particularly the role of Ramsar sites in the long-

term conservation of this population.' Further, Scottish Ministers have recently stated that 'Given the migratory nature of most of the goose populations found in Scotland, it is inevitable that some of the potential future threats to viability will arise in areas outwith the limits of our own national policy framework. Close international collaboration and partnership will be essential if migratory goose populations are to be managed effectively across the entirety of their range' (Finnie & Brankin 2005).

EU Birds Directive

Greenland White-fronts are listed on Annex I of the Birds Directive. This requires Member States to maintain the favourable conservation status of the species through a range of conservation measures and policies. The population is listed as one of a small number of species considered as priorities for funding under the EU LIFE Nature programme, in particular for the development of international plans to help to 'focus on the most urgent and important actions for the different species'. No action has been taken for Greenland White-fronts because 'an international conservation plan has been prepared for this sub-species'. Although prepared, it has never been implemented. The opportunity exists under the Birds Directive, certainly in a British and Irish context, to facilitate joint actions and perhaps beyond that to where the main conservation issues now lie.

Ireland's National Biodiversity Plan (2002–06)

Action 51 (DAHGI 2002) states that: 'Ireland will seek to ensure, in co-operation with other relevant states, that the Greenland White-fronted Goose Conservation Plan is finalised, adopted and implemented.' The interim review of the plan, in early 2005, mindful of the continuing decline in the species since the mid 1990s, commits Ireland 'to renewing contact with Range States to establish a way forward'.

The need to actively deliver these commitments is now more pressing than ever.