The Greenland white-fronted goose Anser albifrons flavirostris in Ireland and Britain 1982/83–1994/95: Population change under conservation legislation

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ORIGINAL ARTICLES

The Greenland white-fronted goose *Anser albifrons flavirostris* in Ireland and Britain 1982/83-1994/95: Population change under conservation legislation

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After protection from hunting on the wintering range in 1982/83, complete surveys of Greenland white-fronted geese at all known Irish and British wintering resorts have been carried out annually. These showed that this population increased by 5.0% per annum from 16,541 in spring 1983 to 30,459 in spring 1995, characterised by a 6.6% annual increase during 1982/83-1991/92, followed by a less rapid increase in subsequent years. In addition, regular counts of at least eight wintering flocks also exist prior to 1982/83. Five of these (including the two most important, Islay in Scotland and Wexford in Ireland) showed no trend before protection, but significant increases after legislation. Two other flocks at protected sites showed increasing numbers prior to changes in legislation, followed by stable numbers afterwards and the eighth flock increased in number before and after protection. On Islay, a significant increase in crude adult annual survival rate (based on census data) occurred after the hunting ban. Numbers on Islay continue to show linear increase. At Wexford, there was no significant difference between crude adult survival before and after the hunting ban where, after a short period of increase, numbers stabilised at 8,000-10,000 after 1990. There were no significant differences in the proportions of young birds before and after protection in these two flocks. Despite overall population increase, seven flocks have become extinct during 1982-1995 and a further five are close to extinction. Eighteen flocks have declined since protection, 35 showed no significant trends and 20 showed increases. Multivariate analysis suggests size, number and quality of feeding areas, levels of disturbance, flock size and latitude influence flock status - smallest most southerly flocks on fewest, poor quality limited feeding ranges showing most serious declines. The consequences of increasing concentration of the population at a few wintering areas need urgent attention and mechanisms should be sought to maintain current range, particularly on traditional semi-natural or low intensity agricultural land.

Key words: Anser albifrons flavirostris, conservation, hunting, protection, white-fronted goose

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The Greenland white-fronted goose *Anser albifrons flavirostris* is one of the world's rarer goose subspecies, breeding in west Greenland and migrating through Iceland in spring and autumn to winter exclusively in Ireland and Britain (Salomonsen 1950). Regular, coordinated counts of wintering numbers do not exist before 1982/83, but from literature sources, Ruttledge & Ogilvie (1979) estimated the world population in the 1950s at 17,500-23,000 birds. They considered numbers to have fallen to 14,300-16,600 by the late 1970s and attributed the decline to wetland habitat loss, disturbance and hunting. These factors, the relatively high mortality rate for the population at that time (Kampp, Fox & Stroud 1988) and the characteristically low productivity of Greenland whitefronts gave considerable cause for concern for the future of the population (Ruttledge 1973, Ogilvie 1978). As a result, protective legislation relating to the Greenland white-fronted goose was changed during the early 1980s (see Fox, Norriss, Stroud & Wilson 1994). In 1982, it was given full protection in Scotland and a three-year hunting moratorium was imposed in the Republic of Ireland. In the winters of 1985/86 and 1988/89, it was hunted at Wexford Slobs, Ireland, under strict bag limitation. Since 1988/89, the moratorium has continued, and no further shooting of geese in the Republic of Ireland has been permitted. In 1985, whitefronts gained protection from hunting in Northern Ireland and, during the spring period when it is most concentrated at staging areas, in Greenland. It remains legal quarry from late summer until April in Greenland although very few are thought to be taken. In 1987, large areas of the breeding grounds were protected by the Greenland Home Rule Government as Wetlands of International Importance under the Ramsar Convention, safeguarding the habitat of an estimated 25% of the summering population (Jepsen, Ragborg & Møller 1996). In Iceland, the species can be hunted in autumn and some 3,000 are taken annually (Sigfusson 1996).

In response to the reported declines and the urgent need for information upon which to base appropriate conservation policy, since winter 1982/83, regular coordinated international counts have been established in Ireland, Scotland and Wales allowing assessment of the numerical trends of all major wintering flocks. Here, we describe the results of the first 13 winters of coordinated counts of the Greenland white-fronted goose population during 1982-1995. Since it is important to understand the influence which changes in protective legislation may have upon the population size and distribution of formerly hunted species, we assess the changes that have occurred since changes in conservation management and protective legislation. We also compare these with trends in counts from eight sites where counts exist prior to protective legislation (1965/66-1981/82), and we analyse post-legislation count data with respect to environmental factors to account for differences in flock trends.

Methods

We defined a 'flock' as a discrete group of wintering geese that used a range of different feeding sites, but which shared a common roost or roosts at some time during the winter (Fox et al. 1994). Two complete counts of all known past and present wintering areas of flocks of Greenland white-fronted geese were conducted each winter during 10 November-10 December and 26 March-10 April. Two days were designated target dates for the count, but when weather or other factors affected accuracy, the most accurate counts (in the opinion of the observer) nearest the census date have been taken. Some flocks were not counted in some census periods in which case data from previous years were substituted but these estimates never contributed more than 1.6% to the total count figures. Observers provided sampled proportions of first-winter birds present in the flocks during autumn or early winter, when they are distinguished from older birds by both lack of white on the face and belly-bars (Cramp & Simmons 1977).

Since 1982, at Wexford Slobs, the single most important Irish wintering site, geese were counted twice during each count period to detect count error due to goose movement between two extensive areas of agricultural land north and south of Wexford harbour. Counts were accepted when they differed by less than 5% from the repeat count. Previous count totals (1967/68-1981/82) involved census of these two areas sequentially, offering the possibility of some limited double counting. Some Irish flocks (especially those on boglands) were highly dispersed and difficult to count. Two flocks in Connemara and southwest Mayo presented particular problems, but were usually covered by one counter in spring and autumn of most years, supplemented by combined aerial and ground counts at five-year intervals.

Earlier counts (1966/67-1981/82) from Islay were conducted over 2-3 days, which assumed no major shifts in feeding distribution on the island between days (Ogilvie 1983). From 1982/83, counts were undertaken by four teams of two people covering the whole island in a single day using predefined routes to ensure best coverage (Easterbee, Bignal & Stroud 1990). These counts are currently carried out by Scottish Natural Heritage as part of their goose monitoring programme, which in very recent years have also supplied data from other parts of Argyll. Counters are requested to record information on a standardised form about the precise location of birds, the habitats used, disturbance and other information which may relate to the conservation status of the birds.

For convenience, we treated the two major wintering areas, Wexford and Islay, as 'flocks', despite these aggregations comprising several subunits of individuals with specific and differing home-ranges (Wilson, Norriss, Walsh, Fox & Stroud 1991). To determine trends in numbers of these and all the other discrete wintering flocks, we carried out regression analysis of log-transformed count data on year for each flock for the period 1982/83-1994/95. We then classified flocks as increasing or decreasing (based on a significant fit to the regression model with a positive/negative rate of change) or stable (where there was no significant fit to the regression model).

A crude assessment of annual adult mortality for Islay and Wexford was feasible given a long run of annual census data and age ratios; however, we restricted the analyses to the 13 years immediately before and the 13 years immediately after legislative protection to compare trends. Using N_t to denote spring census total in year t, and p_t the proportion of young birds, the number of first-year birds can be estimated as $Y_t = N_t \bullet p_t$ and the number of birds older than one year calculated as $T_t = N_t - Y_t$. Crude survival rates can then be estimated as $S_t = T_t/ N_{t-1}$. Where estimated survival exceeded 1.0, it was considered 1.0 in subsequent analyses, although few cases exceeded unity and by very small amounts. These annual percentages of young and crude adult survival were root arc sine transformed to homogenise sample variances and subjected to one-tailed t-tests given the null hypothesis of no increase in productivity or survival after protection from hunting.

For each of these and all the other discrete wintering flocks, we compiled habitat and environmental information to contrast differing trends in the various wintering flocks. These included size of flock at the start of the survey, the latitude of the wintering flock and distance to nearest flock in kilometres (measured between the centre points of two adjacent flocks). Flocks were also classified according to the number and size of feeding sites within the feeding range based on data supplied by counters (Norriss & Wilson 1988). Winter range was classified into three categories: 3) more than 10 feeding sites, generally greater than 500 ha in total extent, 2) three or more feeding sites, generally less than 500 ha in extent and 1) only one or two feeding areas known, usually less than 100 ha. The quality of feeding available to birds within the range of each flock was assessed on the basis of category 3 (i.e. highest quality) for arable stubble and intensively managed grassland, 2) for wet grasslands, callows and semi-improved grasslands and 1) (i.e. lowest quality) for bogland habitats.

The relative use of these habitats based on the information returned by counters on the forms were then used to derive average values for each flock which was then used as an index of habitat quality. Flocks were classified according to the levels of disturbance they were subjected to in the course of the winter according to three categories based on responses to questions relating to disturbance on the count forms returned by counters for each flock: 3) low, geese rarely disrupted from normal patterns of activity or distribution, 2) medium, geese subject to incidental but frequent human disturbance and 1) high, geese habitually moved from favoured feeding areas by human activity. These parameters were then summarised using Factor Analysis (Mardia, Kent & Bibby 1979) and used in a discriminant function analysis (Johnson & Wichern 1992) as a method of predicting whether flocks would be expected to show increasing, stable or decreasing trends on the basis of the environmental parameter values.

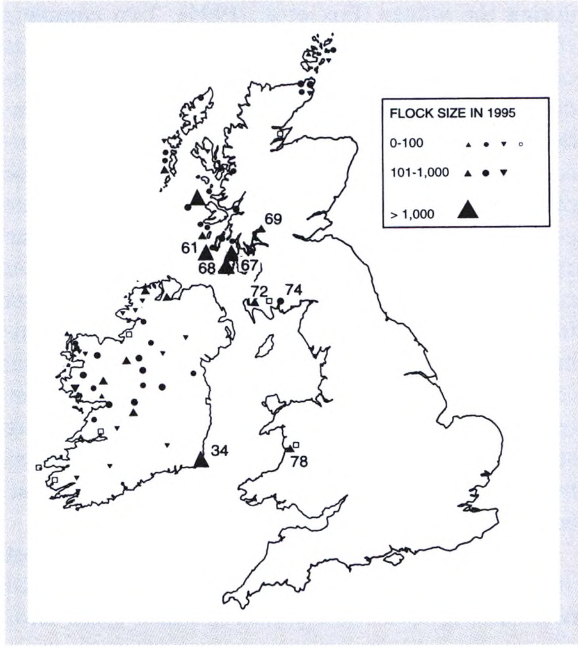

Figure 1. Distribution of wintering Greenland white-fronted Geese in Ireland and Britain in spring 1995. Upwards pointing triangles indicate flocks that have increased during the period 1982-1995, downward triangles indicate declining flocks and circles indicate flocks showing no significant trend. Open squares indicate former locations of flocks which have become extinct in the same period. Digits indicate the following sites mentioned frequently in the text (identified using flock codes from Fox et al. 1994 and listed in Appendix I): 34) Wexford Slobs, 61) Islay, 67) Rhunahaorine, 68) Machrihanish, 69) Loch Lomond, 72) Stranraer, 74) Loch Ken and 78) Dyfi.

Results

Overall distribution and changes in abundance

The distribution of Greenland white-fronted geese as of spring 1995 remains much as previously documented by Ruttledge & Ogilvie (1979), confined to Ireland and western Scotland, with one remaining flock in Wales (Fig. 1). The most important resorts of Islay and Wexford have together supported 59-69% of the world population during 1982/83-1994/95 (Table 1). The overall population increased from 16,500 to 30,500 during this period, recovering from the declines of earlier decades to exceed the previous highest estimates (Fig. 2). On average, total numbers (N) increased by 6.59% per year over the period 1982/83-1991/92 ($r = 0.98$, regression $F = 159.34$, $df = 9$, $P < 0.001$), with numbers apparently beginning to level off at around 29,600 since that time. After a period of initial expansion, the rate of growth in the total population significantly declined ($\ln(N_{t+1}/N_t) = 0.234 - 0.000008N_t$, $r = 0.59$, $F = 5.47$, $df = 11$, $P < 0.05$ for t = 1982/83 to 1993/94 inclusive).

Table 1. Numbers of Greenland white-fronted goose counted during spring censuses in 1982/83-1994/95.

Year	Wexford	Rest of Ireland	Islay	Rest of Britain	Total
1983	6363	2896	3441	3841	16541
1984	6267	3344	4198	3728	17537
1985	7590	3361	4715	4282	19948
1986	7940	3928	5669	4353	21890
1987	7780	4106	6486	4909	23281
1988	8781	4249	7314	4223	24567
1989	9799	4315	6816	5057	25987
1990	9331	3793	7209	5757	26090
1991	9598	4610	8857	6331	29396
1992	9452	4485	9196	6821	29954
1993	8091	4030	10836	4385	27342
1994	10356	4211	9495	5521	29583
1995	9347	4477	9652	6983	30459

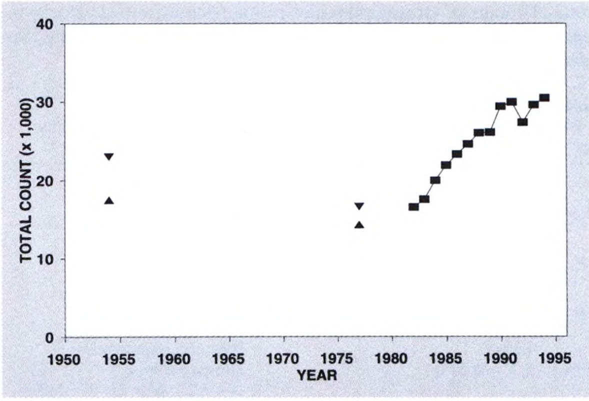

Figure 2. Changes in the estimated numbers of Greenland white-fronted geese. Early totals are the upper and lower estimated range of values from the mid-1950s and late 1970s taken from Ruttledge & Ogilvie (1979). The recent annual counts are the counts from coordinated international surveys described in the text.

Changes in trends in wintering numbers before and after protective legislation

Unfortunately, few Greenland white-fronted goose flocks were consistently counted before and after the change in winter hunting legislation. The data that do exist are summarised below.

Wexford

Prior to the introduction of the shooting moratorium in mid-1982, numbers of Greenland white-fronted geese at Wexford did not increase (0.4% change per annum 1969/70-1981/82, regression $F = 0.39$, $df = 12$, $P = 0.55$; Fig. 3). During 1982/83-1994/95, numbers rose by 3.85% per annum (regression $F = 3.85$, $df = 12$, $P = 0.003$; see Fig. 3). There was no significant difference in the percentage of young before and after protective legislation (mean 16.6% ± 1.7 (SE) for 1969/70-1981/82, mean 17.7% ± 1.9 (SE) for 1982/83-1994/95; $t = 0.42$, $df = 22$, $P = 0.34$; Fig. 4) nor in crude annual adult survival (mean 83.6% ± 2.5 (SE) for 1969/70-1981/82, mean 85.6% ± 3.4 (SE) for 1982/83-1994/95; $t = 0.48$, $df = 22$, $P = 0.64$).

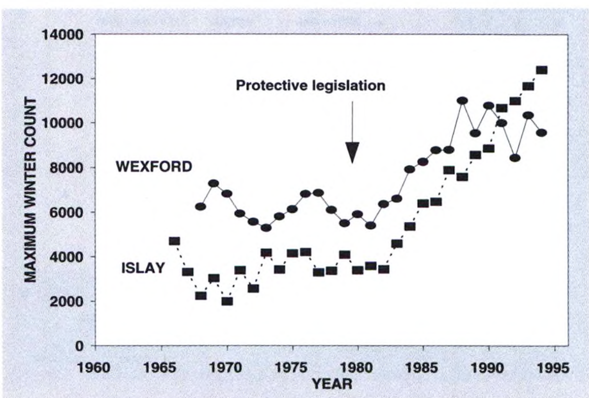

Figure 3. Annual maximum winter counts of Greenland white-fronted geese at their two most important wintering sites, Wexford Slobs (southeast Ireland) and Islay (southwest Scotland), 1969/70-1994/95.

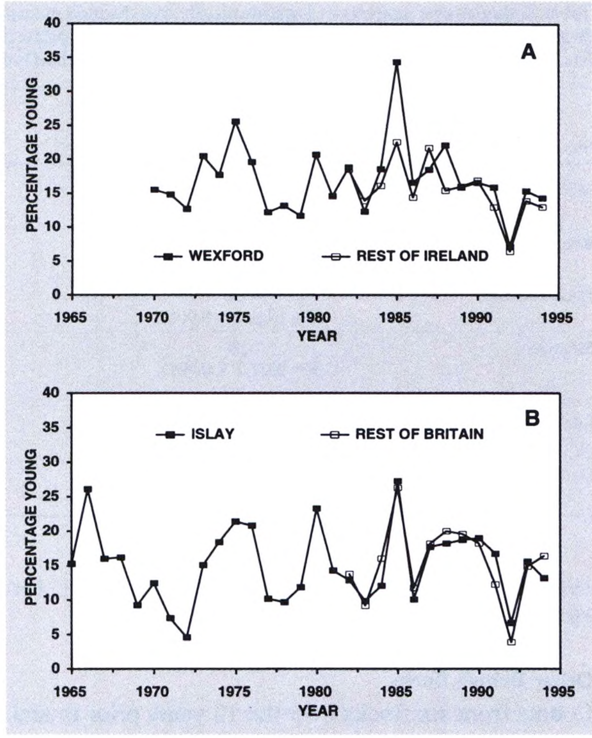

Figure 4. Annual productivity estimates (percentage first year birds sampled) from Greenland white-fronted geese at Wexford and the rest of Ireland (A) and on Islay and from the rest of Britain (B).

Islay

Numbers on Islay showed no increase during 1969/70-1981/82 (i.e. before protection in 1982, 1.00% change per annum, regression $F = 0.43$, $df = 12$, $P = 0.53$). After 1982, there was significant increase in the spring count with time up to 1994/95 (10.00% change per annum, regression $F = 166.55$, $df = 12$, $P < 0.001$; see Fig. 3). There was no significant difference in the percentage of young between the periods before and after protective legislation (mean 14.1% ± 1.7 (SE) for 1969/70-1981/82, mean 15.4% ± 1.6 (SE) for 1982/83-1994/95; $t = 0.60$, $df = 22$, $P = 0.27$; see Fig. 4). There was, however, a significant increase in crude annual adult survival after protective legislation (mean 84.1 ± 4.0 (SE) for

Table 2. Regression analysis of logarithmically transformed maximum annual counts of Greenland white-fronted geese from six flocks in Britain counted regularly before and after the enactment of protective legislation in 1982/83. Note that although a voluntary shooting ban has been self-imposed since 1972 by local wildfowlers on the Dyfi Estuary, the species remains legal quarry at this site.

Site	Annual rate of change, 1969/70-1981/82 (df = 12 in all cases)	Annual rate of change 1982/83-1994/95 (df = 12 in all cases)	Summary change in status between periods
Machrihanish	0% ($F = 0.26$, $P = 0.625$)	7.8% ($F = 55.3$, $P < 0.001$)	No trend, increase
Rhunahaorine	0% ($F = 2.47$, $P = 0.150$)	3.6% ($F = 9.0$, $P = 0.012$)	No trend, increase
Loch Lomond	4.7% ($F = 13.0$, $P = 0.006$)	0% ($F = 2.8$, $P = 0.124$)	Increase, no trend
Stranraer	7.2% ($F = 25.0$, $P < 0.001$)	4.3% ($F = 5.13$, $P = 0.045$)	Increase, significantly slower increase ($t = 4.22$, $df = 22$, $P < 0.05$)
Loch Ken	3.8% ($F = 9.0$, $P = 0.015$)	0% ($F = 0.1$, $P = 0.760$)	Increase, no trend
Dyfi	0% ($F = 0.05$, $P = 0.829$)	6.3% ($F = 75.5$, $P < 0.001$)	No trend, increase

1969/70-1981/82, mean 92.5% ± 2.2 (SE) for 1982/83-1994/95; $t = 2.0$, $df = 22$, $P = 0.03$).

Other British flocks

Counts from six flocks over the 12 years prior to and after the enactment of protective legislation are summarised in Table 2. Numbers from three flocks show an increase after protection following a period with no significant trend (including the Dyfi Estuary, where a voluntary local shooting ban had been in place since 1972, so effectively experiencing no change in protection status). Two flocks using protected areas (Loch Ken, which is partly RSPB reserve and Loch Lomond which is a National Nature Reserve) showed no significant trend after protection following earlier increases. The Stranraer flock showed significant increases throughout, but at a significantly reduced rate after protection.

Trends amongst different flocks during the period under protective legislation

Regression analysis showed significant increases in numbers of 20 flocks, 35 were stable over the period and 18 showed significant decreases (see Appendix I for details). Two apparently new flocks have been established during the review period, namely at Stabannon, Co. Louth, Ireland and at Plockton, near Skye in Scotland. Their numbers have changed little in the six years of data available, so these were included in the stable flocks for the purposes of analysis. In addition, seven flocks have become extinct since 1982/83, namely those in Central Wales, two in Scotland (Bladnoch Valley, Dumfries & Galloway and Loch Eye, Highland Region) and four in Ireland (Inny Valley, Blasket Islands, Fergus & Shannon, Bunduff). Five flocks (Nunton, Western Isles in Scotland and Doo Lough, Lough Barra, Kilcoman and Glencolumbkille in Ireland) are all immediately threatened in the sense that their declining numbers approach extinction.

Relationships between flock status and environmental factors

Increasing, stable and decreasing flocks showed spatial separation based on differences in their scores of environmental factors using Factor Analysis ordination (Fig. 5). Factor 1 was positively correlated with

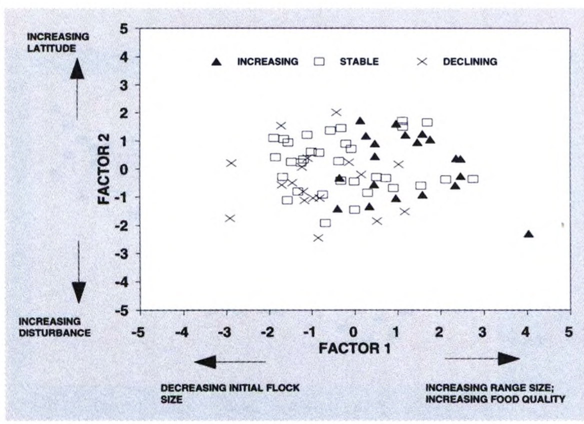

Figure 5. A plot of the scores of the first two factors derived from Factor Analysis of range size, latitude, disturbance index, food quality and initial flock size for 71 flocks/sites of wintering Greenland white-fronted geese. See Table 3 for details of Factor Analysis used to generate this ordination.

Table 3. Variance accounted for by the first two factors used in the ordination of Greenland white-fronted goose wintering flocks (N = 71), based on Factor Analysis of environmental variables for each flock. Correlation coefficients between the first two factors and various environmental variables are also provided, showing levels of significance P < 0.001 as ***.

	Factor 1	Factor 2
Cumulative variance:	0.334	0.528
Correlation coefficients of factors with environmental variables:		
Initial flock size	0.568***	-0.105^{ns}
Range size	0.593***	0.122^{ns}
Latitude	0.032^{ns}	0.767***
Disturbance index	0.239^{ns}	-0.520***
Nearest neighbour	0.124^{ns}	0.246^{ns}
Feeding quality	0.502***	-0.235^{ns}

increasing range size, feeding quality and initial flock size; Factor 2 was correlated with increasing latitude and inversely correlated with increasing disturbance index (Table 3). The mean loadings on Axis 1 of increasing flocks (1.231 ± 0.251 (SE)) was significantly higher than either stable (-0.271 ± 0.214 (SE); t = 4.455, df = 51, P < 0.001) or decreasing flocks (-0.871 ± 0.267 (SE); t = 5.732, df = 36, P < 0.001). There was a significant difference between stable and decreasing flocks (t = 1.713, df = 49, P < 0.05). Mean loadings on Axis 2 of increasing flocks (0.124 ± 0.256 (SE)) did not differ significantly from stable flocks (0.172 ± 0.167 (SE); t = 0.164, df = 51, P > 0.05), but did from decreasing flocks (-0.453 ± 0.272 (SE); t = 1.746, df = 36, P < 0.05); stable and decreasing flocks also differed significantly (t = 2.070, df = 49, P < 0.05).

Table 4. Results of discriminant function analysis used to classify whether Greenland white-fronted goose flocks show increasing, stable or decreasing trends based on the environmental factors shown below. Table cells show actual values down the columns compared with predicted status across the rows.

Predicted state from discriminant function analysis	Actual state: Increasing	Stable	Decreasing
Increasing	16	8	1
Stable	2	16	4
Decreasing	2	9	13
Actual totals	20	33	18
Correctly predicted	16	16	13
% correct	80	48.5	72.2
Linear discriminant functions for groups			
Constant	-448.63	-454.67	-445.62
Initial flock size	6.66	6.39	6.29
Range size	9.51	10.03	10.46
Latitude	15.14	15.36	15.2
Disturbance index	6.98	6.91	7.25
Feeding quality	0.24	-2.35	-3.35
Nearest neighbour	0.1	0.12	0.13

Using the linear discriminant function analysis, 80% of 20 increasing flocks and 72% of 18 decreasing flocks were correctly identified using all six variables, although only 49% of the flocks with no significant trend were correctly identified in this analysis (63% correct classification overall, Table 4).

Discussion

Increases in goose numbers in the Western Palearctic in recent years are primarily considered to be the result of reduced mortality rates resulting from restrictions on hunting (Ebbinge 1991, Madsen 1991). For effective management of goose populations, it is important to understand the effects of legislation upon the abundance and distribution of organisms it is designed to protect. The Greenland white-fronted goose is unique amongst hunted goose species in Europe in receiving large-scale changes in protection measures during the 1980s (a period when monitoring data have generally been of good quality), which gives an opportunity to assess the changes in count data over the period.

Changes in protective legislation and population trends

Overall, the population has increased in number after protection, although there are indications that the rate of increase is now slowing, in contrast to the declines experienced during the previous 20 years (Ruttledge & Ogilvie 1979). It is unfortunate that count data covering the entire population throughout all wintering areas does not exist prior to the changes in hunting legislation. It is also regrettable that the two sources of long-term wintering count data (from Islay and Wexford) were subject to modification of count techniques precisely at the time of the change in legislation, as part of the improvement process involved in the establishment of the complete count coverage. However, the change in counting techniques cannot be responsible for the long-term increase in population since protection was conferred. From the few flocks where count data are available before and after 1982/83, there is some evidence that numbers increased as a result of protection. This is particularly important at Islay and Wexford which together supported around 60% of the total wintering population during 1982/83 - 1994/95 and where goose hunting was common prior to 1982. Increases at these two resorts contributed two thirds of the total increase in the overall population during 1982/83 - 1994/95 (45% on Islay and 21% at Wexford).

The increases at the two major resorts are not explained by increases in production of young over the period, but evidence from Islay, where a few hundred whitefronts were shot every winter prior to protection, shows that crude survival based on census statistics has significantly increased since protection. The data show no such trend from Wexford, although previous analysis of census data showed that adult survival was inversely related to the hunting bag at Wexford and that this relationship was linear, suggesting that this winter hunting mortality was additive to other sources of mortality (Bell 1990). Hence, the cessation of hunting would have been expected to reduce mortality, suggesting some support for the hypothesis that hunting mortality on the wintering grounds may have played a role in population regulation at Wexford. However, the estimation of crude mortality using census statistics is unreliable because of its reliance upon the assumption of constant between-season rates of emigration/immigration. These rates are known to be relatively low amongst marked individuals (Wilson et al. 1991), but the possibility that the increases at Islay and Wexford are not partly explained by increased immigration and/or decreased emigration cannot be ruled out.

Regional differences in trends

What is clear from the results of the census is that whilst the population as a whole has increased during protective legislation, halting the decline in numbers and taking the population away from previously low levels, individual flocks continue to show differing trends, and some continue to be lost. Ringing results demonstrate that wintering flocks comprise individuals from many summer areas, and birds caught together in summer disperse widely in winter despite strong parent-offspring relationships (Fox, Madsen & Stroud 1983, Kampp et al. 1988, Warren, Fox & Walsh 1993). Hence, wintering birds draw from no well defined summering area and given the high degree of between-year site loyalty (Wilson et al. 1991, Warren, Fox, Walsh, Merne & Wilson 1992), the changes in numbers of wintering flocks are more likely to reflect factors operating on the wintering areas than those on the breeding grounds. This seems to be the case, since six environmental factors operating on the wintering grounds could be used to predict flock status (with more than 70% accuracy in the case of declining and increasing flocks). In the last 12 years, Greenland white-fronted geese have shifted to intensively managed grasslands as these have become available. This shift appears to be voluntarily rather than being forced by loss of traditional habitats (Norriss & Wilson 1993). Hence, the relative attractiveness of traditional sites and farmland alternatives may determine habitat use irrespective of protection of traditional habitats. However, habitat loss and disturbance pressures at many flock wintering sites now restrict the range of feeding habitats available to most flocks (Norriss & Wilson 1993). Flocks with very few remaining poor-quality feeding areas which also suffer high levels of disturbance are likely to be most heavily stressed. This is especially true of the few remaining bogland sites, where human exploitation of peatland has fragmented feeding areas and enhanced the relative attractiveness of farmland alternatives (Norriss & Wilson 1993). Hence, for many of the flocks, use of traditional habitats will only be perpetuated on a few large sites where disturbance impacts are limited in the absence of agricultural intensification.

It is not clear why southern Ireland flocks should be declining more than those elsewhere. Two possible explanations could apply. Firstly, although there is no direct evidence, climate change may have resulted in a run of very mild springs in recent years. Most if not all the southern flocks used grasslands for spring feeding, and changed patterns of annual grass production may have increased spring production in such a way that the geese are unable to crop production fast enough to maintain the balance of nutrient content necessary for effective spring hyperphagia. Even if this factor does not cause increased mortality, females may be failing to attain optimal fitness for migration and breeding such that reproductive output declines. Additional support for this hypothesis comes from the fact that all of the flocks involved show within-winter declines in numbers, mainly late in spring, suggesting birds move elsewhere for the critical fattening period prior to departure. Secondly, ringing analysis has shown that birds ringed in the north of the breeding range in Greenland tend to winter in the southernmost part of the wintering range. Hence, these birds experience the most delayed thaw conditions on the breeding grounds (and therefore the most extreme breeding conditions) as well as physically making the longest migration journeys, known to be a key source of goose mortality (Owen & Black

1989). Some elements of the non-breeding population of Greenland white-fronted geese may undertake a northward moult migration within Greenland to take advantage of the delayed thaw and hence delayed plant production to sustain them through the moult period (Salomonsen 1967, Fox & Ridgill 1985). With the increase in the overall population, these non-breeders may increasingly come into contact with the breeding pairs of these northern areas, with possible implications of competitive interactions in such places. In very recent years, Canada geese have colonised and expanded as a summering species in West Greenland (Fox, Glahder, Mitchell, Stroud, Boyd & Frikke 1996), and their presence may place an additional burden on the available food resources of the summering areas in the north of the range.

It is clear that there are multifactorial causes of the differences in trends between different wintering flocks of Greenland white-fronted geese in Britain and Ireland. To fully understand the processes responsible for the observed changes requires examination of the physical and environmental characteristics of the habitats and behaviour of flocks and an investigation of the population processes thus affected. Nevertheless, this initial investigation of time series data does suggest that particular facets of the winter range used by the geese may affect their capacity to increase or maintain numbers. In particular, the sites with low numbers of geese wintering on restricted areas of poor quality habitat show the most dramatic declines. Previous analysis has shown that disturbance can also have an effect (Norriss & Wilson 1988, 1993), especially in concert with restricted range, and there is a tendency for flocks in the extreme south of Ireland to show disproportionate declines and extinctions in very recent years.

Both the UK and Irish Governments have commitments to maintain biodiversity under Article 8 of the Convention on Biological Diversity and to maintain the numbers and range of threatened taxa under European legislation (e.g. Birds and Habitats Directives). Since the maintenance of range of the Greenland white-fronted goose formed a major objective agreed under the Conservation Management Plan for the population (Stroud 1992, 1994), the clear immediate objective is to understand the processes involved which have caused the declines and extinctions of flocks over the past 12 years. Further numerical analysis of the population processes underlying these changes in distribution and abundance are currently underway. This is especially urgent given that most of the flocks concerned are small and hence do not reach the 1% level of population size required to qualify for protection under the Ramsar Convention. It is clear also, that having established the reasons for the declines, some strategic conservation mechanism must be invoked to provide remedial action to support and ultimately enhance the status of these flocks.

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Appendix

Appendix I. Tabulation of data used in the multivariate analysis of trends in Greenland white-fronted goose wintering flocks. Flock numbers and names are the standard ones defined in Fox et al. (1994); initial flock sizes were calculated on the basis of linear regression models of logarithmically transformed flock size on year for each flock. Range, disturbance and feeding quality indices are as defined in the text, latitude defined as decimal values and distance to nearest neighbouring flock measured in km. Flock status was defined in terms of a significant increase (+), significant decrease (-) or stable (0) based on linear regression models of logarithmically transformed flock size on year for each flock.

Flock	Initial flock size	Range	Latitude	Disturbance index	Feeding quality	Nearest neighbour	Flock status
1 Lough Foyle/Swilly	181	1	57.03	3	3.00	38	+
2 Dunfanaghy	102	2	56.17	1	2.85	26	+
3a Sheskinmore	392	2	54.78	1	1.25	19	-
3b Lough Barra bogs	42	3	54.93	2	1.00	26	-
3c Glencolumbkille	50	3	54.67	2	1.29	19	-
4 Pettigo	133	2	54.58	2	2.50	36	0
5 Bunduff	29	3	54.43	1	2.00	28	0
6 Lough Macnean	66	3	54.28	1	1.12	37	0
7 Lough Oughter	24	3	54.03	2	1.00	37	0
8 Caledon	87	3	54.33	3	1.26	54	0
9 Lough Conn	138	2	54.07	3	2.48	22	+
10a Belmullet	15	3	54.23	1	2.00	15	0
10b Owenmore River	20	3	54.15	1	1.00	11	0
10c Carrowmore Lough	27	2	54.15	1	2.05	11	0
10d Owenduff	57	2	54.02	1	1.00	15	-
10e Maumykelly-Altnabrocky	6	3	54.02	1	1.19	11	-
11 Errif and Derrycraff	134	1	53.68	2	1.00	26	0
12 Connemara	112	1	53.40	1	1.00	26	0
13a Rostaff	80	2	53.50	2	1.00	17	0
13b Killower	22	2	53.50	2	1.00	17	0
14 Lower Lough Corrib	72	2	53.35	3	2.10	17	+
15 Rahasane Turlough	51	3	53.22	3	2.35	15	+
16 Tullagher	39	2	52.68	1	2.31	40	0
17 North County Clare	39	2	53.00	3	2.03	17	0
18 Lower Lough Derg	38	2	52.92	2	0.91	17	-
19 Fergus and Shannon Estuaries	74	1	52.70	3	1.25	26	-
20 Lough Gara	206	2	53.93	2	2.00	21	+
21 Drumharlow Lough	117	2	53.98	2	1.78	14	0
22 Loughs Kilglass and Forbes	88	1	53.78	1	2.06	14	+
23 Midland Lakes	365	1	53.58	2	2.87	25	0
24 North Lough Ree	78	2	53.58	2	2.75	15	0
25 River Suck	384	1	53.47	2	2.09	20	0
26 Little Brosna	311	1	53.13	2	2.16	35	+
27 River Nore	82	2	52.90	3	3.00	35	-
28 Kilcolman	32	3	52.25	1	2.40	61	-
29 Doo Lough	172	3	52.03	3	1.00	15	-
30 Killarney Valley	68	2	51.98	1	1.00	15	-
31 Inny Valley	3	3	51.87	2	1.00	33	-
32 Blasket Islands	112	3	52.10	1	2.00	41	-
34 Wexford Slobs	6836	1	52.32	2	3.00	104	+
36 Tankerness/Holm	44	2	58.97	1	2.00	32	-
37 Loons/Ibister	39	2	59.10	2	2.50	18	+
38 Stronsay	65	3	59.14	2	1.48	18	0
39 Westfield	161	1	58.54	2	2.07	12	0
40 Loch Heilen/Loch of Mey	113	1	58.60	2	2.25	7	0
42 Lochs Winless/Wester	91	3	58.22	1	1.00	10	-
44 Loch Eye	23	3	57.74	3	3.00	70	-
45 Loch Urrahag	24	3	58.30	1	2.00	103	0
46 Nunton/Griminish	33	2	57.43	3	2.00	13	-
47 Kilpheder/Askernish	24	2	57.16	2	3.00	21	+
48 Loch Bee	42	2	57.36	2	2.07	21	0
50 Loch Snizort	57	3	57.44	2	1.47	34	-
51 Broadford	33	2	57.17	1	2.03	34	0
53 Muck	30	2	55.78	2	2.00	25	0
54 Loch Shiel	50	3	56.61	1	1.48	25	0
55 Tiree	639	1	56.50	1	2.50	3	0
56 Coll	354	1	56.65	2	2.50	3	+
57 Benderloch	122	2	56.47	1	1.75	48	0
58 Fidden	53	3	56.28	1	1.50	8	0
59 Assapol	31	3	56.28	1	1.50	8	0
60 Colonsay and Oransay	49	1	56.00	1	3.00	18	+
61 Islay	3790	1	55.77	2	2.00	3	+

Flock	Initial flock size	Range	Latitude	Disturbance index	Feeding quality	Nearest neighbour	Flock status
62 Lowlandman's Bay	30	3	55.86	2	2.00	12	0
63 Loch a'Chnuic Bhric	42	2	55.80	1	2.50	3	0
64 Keills and Danna	78	1	55.91	2	3.00	10	+
65 Moine Mhor	60	3	56.04	2	1.50	10	0
67 Rhunahaorine	773	1	55.64	3	2.75	25	0
68 Machrihanish	459	1	55.39	2	3.00	25	+
69 Loch Lomond	141	1	56.07	1	3.00	38	+
70 Bute	60	1	55.78	1	3.00	38	+
72 Stranraer	388	1	54.92	2	3.00	56	+
74 Loch Ken	321	2	55.00	2	2.00	56	0
78 Dyfi Estuary	74	3	52.50	1	3.00	28	+