

Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations

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Abstract

Intensification of agriculture since the 1950s has enhanced the availability, competitive ability, crude protein content, digestibility and extended growing seasons of forage grasses. Spilled cereal grain also provides a rich food source in autumn and in winter. Long-distance migratory herbivorous geese have rapidly exploited these feeding opportunities and most species have shown expansions in range and population size in the last 50 years. Results of long-term studies are presented from two Arctic-breeding populations, the Svalbard pink-footed goose and the Greenland white-fronted goose (GWFG). GWFGs have shown major habitat shifts since the 1950s from winter use of plant storage organs in natural wetlands to feeding on intensively managed farmland. Declines in local density on, and abandonment of, unmodified traditional wintering habitat and increased reproductive success among those birds wintering on farmland suggest that density-dependent processes were not the cause of the shift in this winter-site-faithful population. Based on enhanced nutrient and energy intake rates, we argue that observed shifts in both species from traditionally used natural habitats to intensively managed farmland on spring staging and wintering areas have not necessarily been the result of habitat destruction. Increased food intake rates and potential demographic benefits resulting from shifts to highly profitable foraging opportunities on increasingly intensively managed farmland, more likely explain increases in goose numbers in these populations. The geographically exploratory behaviour of subdominant individuals enables the discovery and exploitation of new winter feeding opportunities and hence range expansion. Recent destruction of traditional habitats and declines in farming at northern latitudes present fresh challenges to the well being of both populations. More urgently, Canada geese colonizing breeding and moulting habitats of white-fronted geese in Greenland are further affecting their reproductive output.

Keywords: agricultural change, *Anser albifrons flavirostris*, *Anser brachyrhynchus*, grassland management, reproductive success, wetland loss

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Introduction

Of the total European Union land area in 2001, 43% was devoted to agricultural production, more in some

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states (e.g., 57% in the Netherlands, 63% in Denmark, 64% in Ireland and 70% in UK; FAOSTAT, www.fao.org). Large areas of Europe are now devoted to production of food and raw materials, replacing many natural habitats used by birds. Nevertheless, the agricultural production area of Denmark, the Netherlands, Belgium, Ireland and the UK fell by 14–22% between 1961 and 2001 (FAOSTAT). However, the ‘green revolution’ has increased productivity in remaining areas, producing 25% more food per capita than 30 years ago (Krebs *et al.*, 1999), at a cost to farmland species richness, especially among birds (Pain & Pienkowski, 1997; Siriwardena *et al.*, 1998; Krebs *et al.*, 1999). Modern agricultural development is thus equated with reductions in avian abundance and distribution, which continues through improvements to cultivation methods (e.g., Donald *et al.*, 2001). By contrast, herbivorous migratory waterbirds have benefited from the spread of, and recent changes in, agriculture, especially larger species, such as geese and swans (van Eerden *et al.*, 1996; Abraham *et al.*, 2005; Gauthier *et al.*, 2005). Selective breeding and improved management have enhanced grass quality throughout Europe since the 1950s, elevating crude protein content, increasing digestibility and prolonging growing seasons (van Eerden *et al.*, 1996, 2005). Agricultural policy has driven large-scale cultivation patterns that have created extensive areas of largely uniform, intensively managed areas of grassland and cereals. This has increased the carrying capacity of the European land mass for true grazing birds and several northern nesting geese have shown dramatic spatial redistribution and increases in population size in the last 50 years (Madsen *et al.*, 1999). How have changes in goose distribution and abundance resulted from shifts in habitat use? In particular, have geese gained fitness benefits from moving from exploitation of seminatural habitats along an agricultural intensification gradient to increasingly managed grasslands and arable crops?

In this paper, we examine patterns of abundance, distribution and habitat use from long-term studies in two populations of Arctic-nesting geese along this transition gradient. The Svalbard-nesting population of pink-footed geese (PFG), *Anser brachyrhynchus*, winters in Belgium, the Netherlands and Denmark, staging in spring and autumn in Norway (Madsen *et al.*, 1999). The Greenland white-fronted goose (GWFG), *A. albifrons flavirostris*, breeds in west Greenland, migrates via Iceland in spring and autumn to wintering areas in Ireland and the United Kingdom. We assess fitness consequences to geese of exploiting alternative habitats simultaneously, in order to understand the observed shifts in habitat exploitation, and in an attempt to

comprehend how these may contribute to increases in global population size.

Materials and methods

Survey

The PFG has been subject to an annual co-ordinated winter survey in Belgium, the Netherlands and Denmark since 1965 (Madsen, 1982; Ganter & Madsen, 2001), the GWFG in Ireland and Britain since 1982 (Fox *et al.*, 1998b). Age ratios have been sampled among both populations based on plumage differences of first winter birds (Cramp & Simmons, 1977); since the 1980s; data are available from most wintering flocks of GWFG on an annual basis, although not consistently from all sites in Ireland since 1992 (Fox *et al.*, 1998b).

Capture-mark-recapture

PFG have been captured annually in Denmark and GWFG in Ireland and fitted with conspicuous plastic neck collars bearing unique engraved codes (PFG since 1990, GWFG since 1983). Both populations have been subject to intensive resighting programmes throughout their ranges to study habitat and site use, site fidelity, lifetime reproductive output and annual survival.

Habitat use

PFG habitat use has been assessed during various projects in Denmark. During 1980–1983, habitat affiliation of each flock was registered in a bimonthly national survey (Madsen, 1984); during 1993–1995, winter and spring habitat use was recorded at weekly intervals at key sites in west Jutland (Madsen, 1996; J. Madsen, unpublished results). During winter and spring 1999–2002, habitat use of individually marked geese was registered daily in central feeding areas in west Jutland (J. Madsen, unpublished results). Bimonthly counts carried out in Belgium since 1959 have been used to describe changes in PFG regional distribution and abundance in relation to agricultural land-use and conservation measures (Kuijken, 1969, 1972, 1975, 1988; Meire *et al.*, 1988; Meire & Kuijken, 1991; Kuijken *et al.*, 2001).

GWFG habitat use at one of the two most important wintering sites (Wexford Slobs, south-east Ireland) was assessed by observations of field use by marked individuals since 1983/1984 (see Fox, 2003). Habitat use by wintering GWFG flocks was assessed at least twice annually based on a standard habitat classification (Fox *et al.*, 1998b). GWFG have increasingly used intensive agricultural land in preference to natural and

seminal habitats (Norriss & Wilson, 1993; Fox *et al.*, 1998b). We tested the consequences of this change for reproductive success among flocks, comparing the level of use of intensively managed agricultural land with the mean proportion of young of each wintering flock in Britain and Ireland during 1982–1992. Agricultural intensity was expressed in terms of a food quality score, assigned as 1 for flocks using peatland habitats (i.e. lowest quality), 2 for those using wet grasslands, floodlands and semi-improved grasslands and 3 for flocks using arable stubble and intensively managed grasslands (i.e. highest quality). The relative use of these habitats based on information returned by the counters at the point of encounter during each census was then used to average values for each flock (Fox *et al.*, 1998b). Because of interannual variation, only those flocks with nine or more age ratios available from 11 years were included. Marked birds show very high levels of between-winter site fidelity (Wilson *et al.*, 1991). Hence, assuming that they rely on endogenous reserves for reproduction (Gauthier *et al.*, 2003), an inverse relationship between breeding success and use of farmland habitats is expected if an agricultural diet fails to fulfil the nutritional needs of the geese.

Results

PFG

Population status and trends. The PFG population increased from 12 000–20 000 to 40 000–50 000 from the mid-1960s until 2003 (Fig. 1); the rapid increase in the 1970s was attributed to improved survival because of relaxation of winter shooting pressure (Ebbing *et al.*, 1984). The population continued to grow through the 1980s and 1990s, but has been showing signs of levelling off since the late 1990s (based on capture-recapture estimation, Ganter & Madsen, 2001; J. Madsen, unpublished results).

Changes in wintering and staging range. In the early 1980s, PFG migrated directly from Svalbard to autumn-staging areas in Denmark, and to discrete wintering grounds in Friesland in the Netherlands and Belgian Flemish Polders. In spring, the population was concentrated in only 12–14 areas along the west coast of Denmark. When migrating to the breeding grounds, the geese stopped over in Vesterålen-Lofoten in north Norway (Fig. 2).

During the 1980s, two new spring-staging areas were established; one in north-west Jutland, Denmark and one in Trøndelag, mid-Norway. In the subsequent decade, these new regions experienced a dramatic expansion in geese numbers that affected spatial and

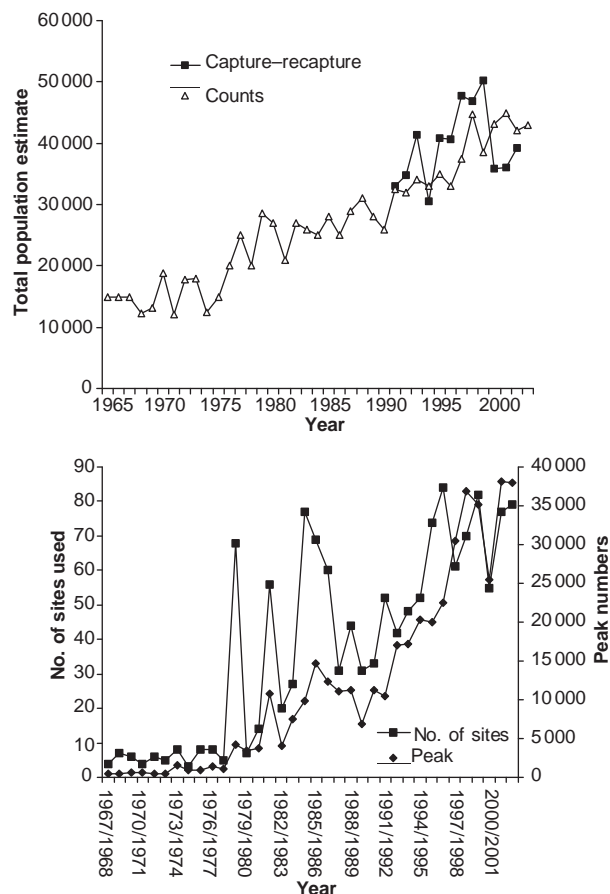


Fig. 1 Changes in abundance of the Svalbard pink-footed geese population, 1965–2003 (upper), derived from population counts and estimates based on capture-mark-recapture analysis (1991–2002). Lower graph shows peak numbers of pink-footed geese wintering and the number of sites used in Belgium, 1967/1968–2002/2003. Most sites lie adjacent to each other. Geese increased the number of sites used during cold winters (e.g., 1978/1979, 1984/1985, 1995/1996 and 1996/1997). Sources: Madsen *et al.* (1999), Ganter & Madsen (2001), J. Madsen, Berg, E. Kuijken, F. Cottaar & B. H. Larsen (unpublished results).

temporal use of sites. Both the above regions were used during autumn migration, and later in the decade, new autumn and spring staging areas also became established in south Norway. Increasing numbers (490% in December–January) now spend a greater part of the winter in Belgium and the range has expanded from the original core area there (Fig. 2, Meire & Kuijken, 1991; Kuijken *et al.*, 2001). The number of spring sites used in Denmark has increased to 32–35.

Changes in habitat use – winter. Before the mid-1980s, PFG generally stayed south of areas experiencing subzero temperatures in winter, moving north or south in immediate response to temperature conditions, but mainly feeding on grasslands in

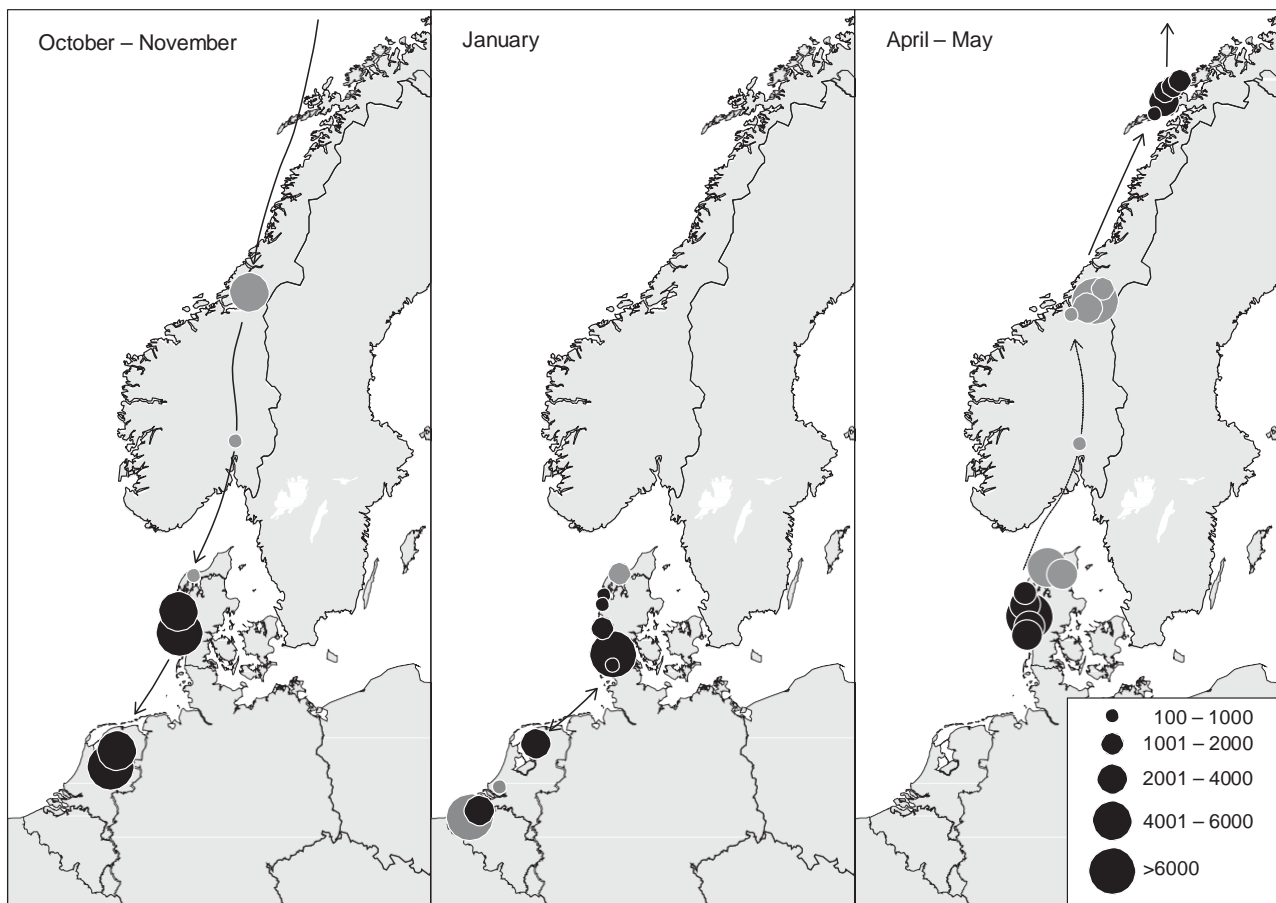


Fig. 2 Sites used by pink-footed geese during autumn, winter and spring in 1980–1983 (black dots) and 2000–2003 (new sites shown by shaded dots). Dots represent average seasonal peak numbers. Arrows indicate migration routes.

Belgium and the Netherlands (and Denmark only in mild winters). Since then, an increasing proportion of the population has stayed in Denmark, even during severe winters, where increasingly they have fed on young cereal plants (Fig. 3). While temperatures remain above freezing point, most geese feed on grasslands, but below 0 °C, geese switch to winter cereal fields (Therkildsen & Madsen, 2000). Below freezing point, leaves of pasture grasses decrease in quality (measured by nitrogen content), whereas those of winter wheat remain stable. Even below 0 °C, PFG can balance their daily energy budgets feeding on winter cereal plants (Therkildsen & Madsen, 2000).

The change in habitat use and northward shift in winter distribution coincided with the increase in winter cereals grown in Denmark (which tripled from the early 1980s to early 1990s under the national plan to reduce the nutrient runoff from farmland, Fig. 3). Winter cereals have replaced spring-sown cereal cultivation, whereas the area of seminatural grassland and pastures has remained stable (StatBank Denmark, the on-line national repository for Danish agricultural statistics

<http://www.dst.dk/>, data published annually, the latest can be found in Danmarks Statistik, 2002).

In Belgium, conversion of wet seminatural grasslands to arable land has reduced the extent of traditional goose habitats. There, PFG increasingly feed on winter wheat, silage grass and maize stubble (Kuijken *et al.*, 2001), although increased use of croplands has delayed changes in agricultural land use (Kuijken, 1988; Dumortier *et al.*, 2003). The PFG preference for grasslands has resulted in a range expansion, resulting in the exploitation of previously unoccupied coastal polder grasslands. Wintering numbers have increased despite concurrent increases in Denmark (Fig. 1).

Changes in habitat use – spring staging in Denmark. In the early 1980s in Denmark, the majority of spring-staging PFG foraged on seminatural grasslands, pastures and salt marshes, also gleaning grain from the surface of newly spring-sown cereal fields at a few farmland sites. To reduce grain loss in newly sown fields, the Ministry of Agriculture initiated a baiting programme in the

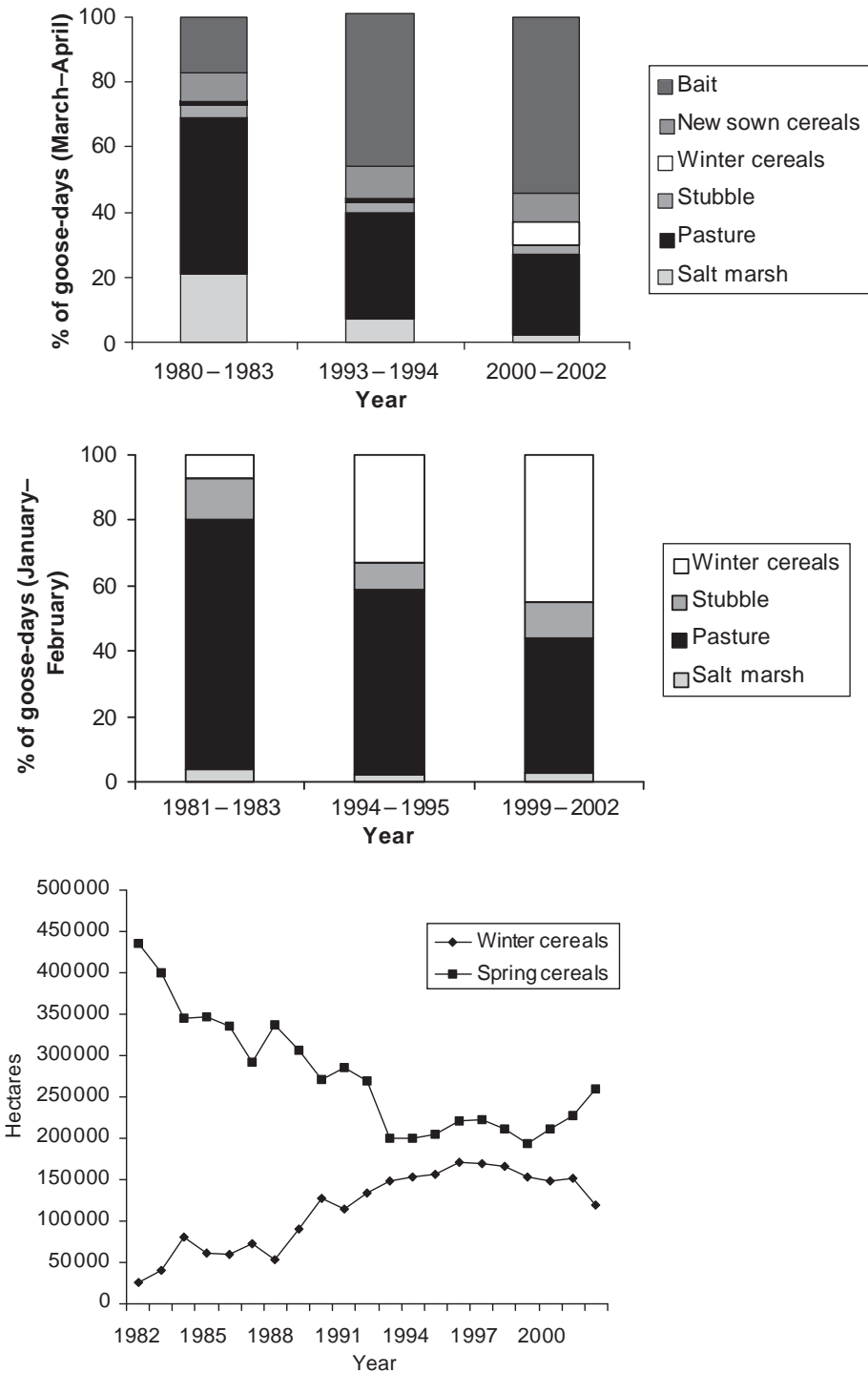


Fig. 3 Upper: winter (January–February, upper) and spring (March–April, middle) habitat use by pink-footed geese in Denmark during three periods between 1980 and 2002, expressed as the proportion of total goose days spent in each category. Lower graph shows area of spring- and winter-sown cereals in Ribe, Ringkjøbing and Viborg counties, West Jutland, Denmark, 1982–2002. Sources: Madsen (1984, 1996; J. Madsen, unpublished results) and Danmarks Statistik (2002).

early 1970s, provisioning grain in certain grassland fields to attract geese at one site. The habit of feeding on newly sown grain spread to other sites along the

Danish west coast, so baiting was introduced at four additional areas from the late 1980s. By the early 2000s, nearly 60% of the geese were feeding on bait or newly

sown fields, with a proportional decline in goose use of grasslands, and especially salt marshes (Fig. 3). Given the overall population increase during this period, this means that while the absolute use of grasslands increased over the period, that of salt marsh habitat actually declined.

The increase in use of newly sown fields has occurred despite a decrease in their extent in west Jutland (Danmarks Statistik, 2002). There is no indication that the quality of salt marshes or seminatural grasslands has decreased (e.g., because of reduced stock grazing pressure). On the contrary, at one reserve (Tipperne, heavily used by PFG in the 1970's) grassland management significantly improved goose-grazing opportunities (Madsen, 1980), yet numbers fell in the 1980s and at present, the area is hardly used by PFG in spring because of improved foraging opportunities elsewhere.

Changes in habitat use - spring staging in Norway. On spring staging sites in Vesterålen, north Norway, geese have geographically limited feeding opportunities along the coasts of mountainous islands. Traditional spring-feeding habitats were formerly salt marshes and pastures, but since the 1980s, geese have almost abandoned salt marshes, which have become overgrown because of reductions in hay cutting and livestock grazing. In Vesterålen, pastures have become more intensively farmed with increased fertilization and reseeding. However, in recent years, farming practice has become polarized, with highly intensive pasture management in core areas and abandonment of pastures in peripheral areas (Tombre *et al.*, submitted). Increasing conflicts between farming interests and PFG, especially in the most intensively farmed areas, have resulted in organized scaring with a consequent reduction in geese use of key sites in Vesterålen (Tombre *et al.*, submitted). Since the early 1990s, increasing numbers of PFG also stop in Trøndelag, mid-Norway, where they sequentially exploit a mixed farmland with stubble, pastures and newly sown cereal fields in spring (Madsen *et al.*, 1999).

Changes in fitness measures. The daily energy budgets (i.e. daily energy intake and consumption) were compared for PFG feeding on Danish seminatural grasslands and newly sown cereal fields during spring. Energy intake rates were higher, consumption lower and changes in fat index higher in newly sown fields compared with grasslands, resulting in an energy balance in grasslands and a highly positive budget in newly sown fields (Madsen, 1985 although protein acquisition was not quantified). Hence, the increasing use of grain during spring (both through increased

feeding on newly sown fields and artificial provision of grain) generally improved the body condition of geese prior to the onset of migration (J. Madsen, unpublished results) and consequently may have contributed to the population increase.

GWFGs

Population status and trends. Small population size, restricted world geographical range and decline during the 1950s–1970s (to ca. 16 600 birds by 1982) focused considerable nature conservation attention on the GWFG in the 1980s (Ruttledge & Ogilvie, 1979; Fox *et al.*, 1998b) and led to its protection from winter hunting from 1982 (Fig. 4, Fox, 2003). The nature and rate of increase following protection at the most important wintering site, Wexford Slobs in SE Ireland, was consistent with the hypothesis that local hunting mortality was completely additive in that population, suggesting hunting kill had limited the size of the population there, and probably elsewhere (Fox, 2003). This increase continued until 1999, when the population peaked at 35 600 birds; since then numbers have shown a rapid decline (Fig. 4), consistent with stable annual adult survival, but a long-term decline in reproductive success, which now fails to replace annual losses in the population (Fox, 2003).

Changes in wintering and staging range. The more than doubling of the population between 1982 and 1997 brought no change in the extent of winter range of GWFG (Fox *et al.*, 1998b; A. D. Fox *et al.*, recent unpublished results). Three new winter localities were

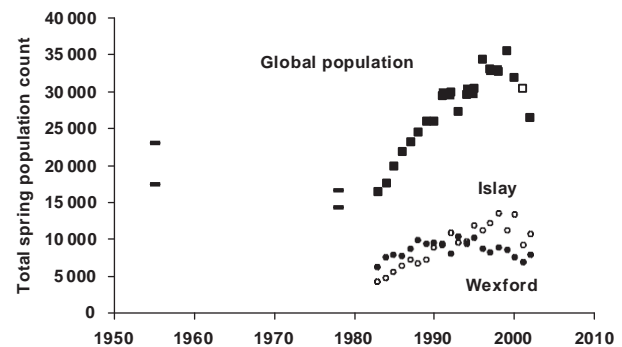


Fig. 4 Total spring counts of Greenland white-fronted geese at all known resorts (filled squares) during 1982/1983–2001/2002. The count for spring 2001 (unfilled square) is missing because of Foot and Mouth Disease restricting access in that year, and was modelled from the previous autumn count. Horizontal lines indicate upper and lower population estimates of Ruttledge & Ogilvie (1979) for the population in the late 1950s and late 1970s. Spring counts for the two major wintering sites, Wexford Slobs (filled circles) and Ilay (unfilled circles), are also shown.

briefly colonized by GWFG between 1982 and 2001 outside the previously known range, but none persisted to constitute permanently colonized sites. In Iceland too, the same areas are apparently used as in former times, with agricultural feeding areas associated with traditionally used core roost sites. Unlike the PFG, there has been no expansion into previously unoccupied areas, even though GWFG have exploited novel habitats within the previously occupied range.

Changes in habitat use – winter. The GWFG traditionally wintered on oceanic blanket mires and raised bog systems with pronounced surface patterning and locally abundant cotton grass, *Eriophorum angustifolium*, and white-beaked sedge *Rhynchospora alba*, favoured dietary items of the subspecies (Ruttledge, 1929; Cadman, 1953; Fox & Stroud, 2002). Although widespread in Europe, *E. angustifolium* exploitation by wintering GWFG was confined to ‘quaking’ *Sphagnum* lawns and permanently inundated areas subject to mean January temperatures 43 IC (i.e. Ireland and western Scotland). Here, absence of winter frost and the soft substrate enabled geese to extract and consume the lower stem base, the belowground over-wintering storage organ of *Eriophorum*, rich in sugars and nonstructural polysaccharides (Phillips, 1954; Shaver & Billings, 1976; Fox & Stroud, 2002). These dietary and habitat microtopographical requirements explain the highly restricted historical winter distribution, defined by the climatic template for the formation of patterned mire ecosystems, further restricted by largely frost-free conditions in winter. Further north, surface freezing precludes extraction of plant organs by geese in winter, while such habitats are rare in France where lower rainfall and higher temperatures mitigate against peatland formation.

In the 1950s, 49% of all known ($n = 596$) flocks at that time exploited peatlands to some extent, although this had fallen to 45% (29 out of 65) by the 1970s (Ruttledge & Ogilvie, 1979). Despite over 80% loss of traditional patterned oceanic mire habitat in the last 100 years within its winter range, the GWFG continued to feed on peatland vegetation in the late 20th century and into the early 21st century (Fox *et al.*, 1998b; A. D. Fox *et al.*, unpublished results). Even where all daytime feeding takes place in agricultural habitats, many flocks still use peatland habitats as night-time roosts, where supplementary feeding occurs. However, by 1995, only 12 out of 74 (16%) flocks consistently used peatlands in winter, all but one in Ireland of which exhibited stable or declining population trends (Fox *et al.*, 1998b). That number is since thought to have declined further. Hence, there is no evidence to suggest that geese have been forced away from natural habitats

by increasing local densities into suboptimal farmland habitats.

At Wexford (typical of flocks utilizing intensively managed farmland in winter), GWFG utilize reseeded grass leys throughout the winter, supplemented by gleaning grain from cereal stubble and other crops during the first half of the winter and root crops (especially sugar beets) in mid-winter (Fig. 5). Despite the predominant use of grass, GWFG have tended to use stubble and beet proportionally to a greater extent since the mid-1980s (Fig. 5, but also in absolute terms).

Changes in habitat use – spring staging in Iceland

GWFG rapidly recoup depleted endogenous stores (consumed during spring migration from wintering areas in Britain and Ireland) in Iceland in preparation for the onward migration over the Greenland icecap to breeding areas in West Greenland (Fox *et al.*, 1999, 2003). Before major human impacts on natural plant communities, spring-staging geese fed on the below-ground storage organs of *E. angustifolium* and Lyngby's sedge *Carex lyngbyei*, extracted from the soft wetland substrates (Francis & Fox, 1987; Fox & Stroud, 2002). In the southern and western lowlands almost all (497%, Icelandic National Report to Ramsar Convention, 1998) natural Icelandic wetlands have been modified by drainage. Although irrigation to grow *C. lyngbyei* for winter hay created a suitable goose habitat in the early part of the 20th century, this practice was abandoned through the 1940s and 1950s. This period marked the start of very extensive wetland destruction, through drainage and the creation of new dry hayfields, a practice that continued until the early 1980s (A. D. Fox *et al.*, unpublished results). Despite these changes in land use, staging GWFG have adapted to new conditions without apparent fitness costs, in terms of changes in reproductive success at that time (A. D. Fox *et al.*, unpublished results). More than 80% of spring staging GWFG exploit artificial agricultural habitats (Francis & Fox, 1987), mostly feeding upon the early growth of grasses, especially a Norwegian cultivar of *Phleum pratense* (Fox *et al.*, 1998a). These provide high-quality forage (even in subzero temperature) before the availability of traditionally used wetland species, which remain inaccessible (because of frozen ground) until after the last frosts (Nyegaard *et al.*, in press; A. D. Fox *et al.*, unpublished results). Since 1980, quotas have reduced sheep numbers in Iceland (and hence fertilizer use), although the area of hayfields has been more or less constant since that time (A. D. Fox *et al.*, unpublished results). It is unknown whether artificial grasslands provide all the necessary nutritional

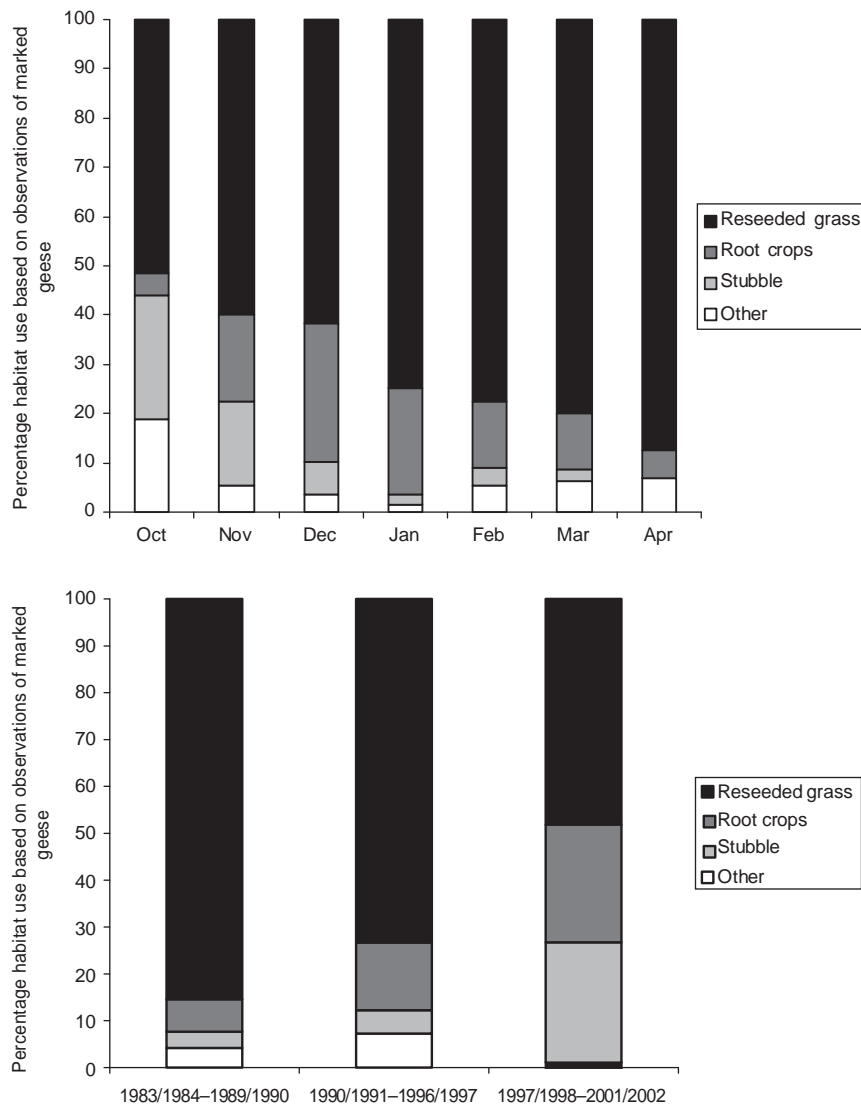


Fig. 5 Winter use of farmland habitats by Greenland white-fronted geese at Wexford, south-east Ireland, based on 64 930 observations of marked individuals. Upper graph shows overall within-season changes during the years 1983/1984–2001/2002, lower graph shows changes in overall habitat use over this period (sample sizes for the three time periods were 39 172, 19 303 and 6 455, respectively).

requirements of spring staging geese; however, their ability to successfully adapt to such habitats suggests that they do (Nyegaard *et al.*, in press; A. D. Fox *et al.*, unpublished results). It may be necessary in the future to maintain grassland management in key Icelandic spring stopover areas to support geese, especially as livestock numbers continue to fall.

Changes in fitness measures. The positive correlation between the mean proportion of young and feeding-quality index of vegetation among Irish and British wintering GWFG from 1982 to 1992 (Fig. 6) supports the hypothesis that breeding success was highest among flocks mainly using improved agricultural habitats

compared with those using seminatural and bog habitats in winter. These flocks contribute many more young than do those exploiting less managed habitats and were consistently those flocks that showed greatest increase in number (Fig. 6).

Discussion

In the past 60 years, agricultural developments have led to a loss of bird populations, but northern breeding geese stand out as an exception. The Anatidae first encountered, and probably adapted to, emerging agricultural practice in Western Europe 2500 years ago, when cereal and bean cultivation first offered

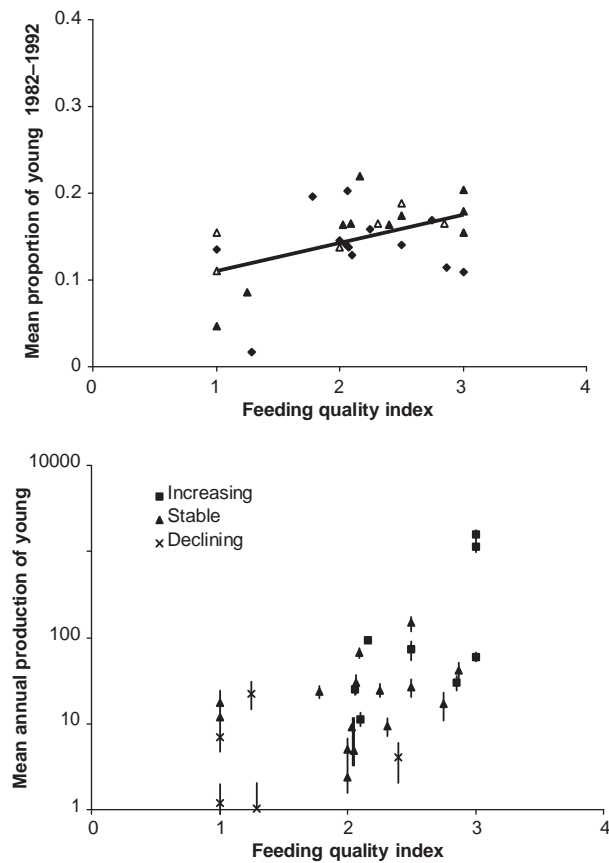


Fig. 6 Relationship between the feeding range quality index and average annual breeding success (percentage young, upper graph) of wintering Greenland white-fronted goose flocks in Ireland and Britain, 1982-1992 ($r = 0.42$, $F = 55.9$, $P = 0.022$). Filled triangles represent sites with values from all 11 years, open triangles from 10 years and diamonds from 9 years. Methods for the compilation of the feeding range quality index are described in Fox *et al.* (1998a) and range from 3 (birds feeding exclusively on arable stubble and improved grassland) to 1 (birds feeding exclusively on bogland habitats). Flock values are listed in Fox *et al.* (1998a, Appendix 1). Lower graph shows the mean (\pm SE) annual number of young contributed by each of the flocks shown in the upper graph (during 1982-1992, note logarithmic scale). This confirms the minor contribution (and stable and declining trends during a period of overall population increase) of bogland flocks using traditional habitats to the overall reproductive output of the population as a whole.

crude autumn stubbles as a food source (van Eerden *et al.*, 1996) and Roman hay cultivation later attracted grazing waterbirds (Owen, 1980). Improved farming systems and climate amelioration during 690-760 AD may have resulted in an upsurge in goose visits to farmlands (Kear, 2001). Our results confirm the substantial changes in grassland agricultural practice that have occurred since the 1950s, with greatest consequences for herbivorous waterbirds, especially through

the creation of extensive areas of intensively managed grasslands (Owen, 1976; Rutschke, 1987). The GWFG described here, exploiting peatland and inundation habitats, was unusually late in adapting to agricultural habitats.

Geese are relatively long-lived birds exploited by humans as a food source. Hence, release from the effects of additive hunting mortality (Gauthier *et al.*, 2001; Menu *et al.*, 2002, including GWFG Fox, 2003) has contributed to their recent rapid increase in the Northern Hemisphere. In the last three decades, the PFG population has doubled in number. The initial increase in the 1970s was attributed to declining hunting pressure, whereas the subsequent increase (into the late 1990s) cannot be related to specific episodes of protection or management measures affecting survival rates. From the early 1980s until the late 1990s, annual breeding success has been variable, but without trend (average 1980-1997: 16.7% juveniles). Annual adult survival was relatively high in the early 1990s (0.85-0.90), but decreased to 0.79 by the late 1990s (Madsen *et al.*, 2002). The causal relationships behind these changes are not clear, but one explanation may be an escape from potential density dependence during winter and spring because of the changes in habitat use, which may have improved both winter survival and opportunities for accumulation of body stores prior to breeding. In the case of the GWFG, the evidence is clearer. Under protection from additive hunting mortality, the population increased, generally faster at sites where flocks exploit high-energy agricultural crops. The significantly higher production of young among those groups compared with flocks wintering on seminatural and natural habitats supports this conclusion.

Very few populations breeding in Arctic ecosystems still exploit the traditionally used natural winter habitats. The GWFG gives a unique opportunity to simultaneously observe the transition from exploiting natural wetland wintering habitats to feeding on low intensity agricultural grasslands to gleaning grain postharvest and grazing on intensively managed grasslands. Plant breeding has been successful in producing grasses with high crude protein and energy content as well as high digestibility. Grain of the highest quality, modern sowing techniques, growth regulators, fertilizers and pesticides further ensure food production at increasing plant densities, thereby enhancing food intake rates for geese. Among PFG, this transition has increased goose energy intake rates in the nonbreeding season and in the GWFG, it is also associated with enhanced reproductive output. Hence, the spatial and temporal transitions in goose behaviour apparently have a demographic explanation, whereby geese

increasingly exploit energetically more profitable sites, rather than necessarily being forced there by other mechanisms (e.g., habitat destruction, Norriss & Wilson, 1993).

The agricultural landscape is highly seasonal, with concentrated periods of growth, harvest and protracted dormancy. In Europe, geese have become highly dependent on the agricultural landscape as their 'survival habitat' (sensu Alerstam & Högstedt, 1982). The dynamic agricultural seasonality and changes in cropping practice may have been selected for adaptability among goose populations. The GWFG traditionally exploited a highly predictable resource (locally abundant storage organs of peatland plants available throughout the winter) which favoured a high degree of site fidelity (Wilson *et al.*, 1991; Fox *et al.*, 2002). In contrast, the Svalbard PFG, as well as the Iceland and Greenland-breeding PFG population wintering in Britain, show a seasonal pattern of movement along a corridor of winter feeding opportunities (Newton & Campbell, 1973; Madsen, 1984; Fox *et al.*, 1994). The seasonal predictability of agricultural production on large spatial scales contrasts with the unpredictability at farm and field levels. Accordingly, selection for traits favouring site fidelity to a general region coupled with local exploratory behaviour is highly advantageous, and has probably been developed in goose populations with longest associations with agriculture. Exploratory behaviour is most marked among subadult (i.e. subdominant) individuals within goose populations, normally displaced from optimal feeding opportunities by behaviourally dominant individuals (Stahl *et al.*, 2001). For these individuals, more exploratory behaviour does not necessarily incur fitness costs, since 'exploratory' individuals among wintering Svalbard PFG did not show any difference in abdominal profile scores (an index of body fat stores) compared with dominant and sedentary individuals (Madsen, 2001; B. Ganter & J. Madsen, unpublished results). Such asymmetry in competitive ability among individuals has, therefore, provided these large migratory herbivores with a potential behavioural mechanism for the population to rapidly discover and exploit new feeding opportunities. This plasticity has likely played a role in the geographical expansion of winter range, which has enabled further numerical expansion in populations showing this trait (such as the Svalbard PFG), but not in those showing greatest site fidelity (e.g., GWFG).

Interspecific competition as a result of range extensions

One poorly studied consequence of recent expansions (and consequent temporal and spatial overlap) in number and distribution of northern nesting geese is

the degree to which interspecific interactions increasingly occur. Where these interactions are asymmetric in nature, effects on local distribution and abundance may ultimately have demographic consequences (e.g., where the subordinate species may lose access to favoured feeding areas because of the aggressive nature of the dominant). Although not formerly presented here, an important footnote to this presentation relates to the recent relatively rapid decline in number of GWFG since the peak count of 35 600 in 1999 (Fig. 4). This decline is entirely consistent with stable survival (confirmed by survival estimates based on capture-mark-recapture at Wexford, where wintering numbers declined prior to those elsewhere), but long-term declines in breeding success (Fox, 2003). The population presently simply fails to produce enough young to balance annual losses (A. D. Fox *et al.*, unpublished data). Analysis to be presented elsewhere strongly suggests that there are no obvious relationships between breeding success and agricultural management of Icelandic staging areas, density-dependent factors or climate change to explain this trend. The population of Canada geese *Branta canadensis interior*, nesting in northern Quebec and wintering in eastern United States, benefited from several years of partial protection from hunting there in the 1990s. It 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, white-fronted geese fed more on low-quality moss species and showed lower intake rates in sympatric situations with Canada geese than in allopatry, and Canada geese were behaviourally dominant over white-fronted geese in all observed encounters (Kristiansen & Jarrett, 2002). Since the late 1980s in one regularly surveyed area, Canada geese have displaced the endemic species from territories where it was formerly the only goose species present (Kristiansen & Jarrett, 2002). Aerial surveys of extensive areas showed that in spite of favouring the same geographic region, the two species were less likely to occur together than by chance, suggesting some segregation at a large spatial scale (Malecki *et al.*, 2000). Re-survey of breeding areas in 2003 confirmed continuing extensive loss of former breeding territory to the colonist species (J. Madsen, unpublished data). The apparent robustness of the GWFG to adapt to novel feeding opportunities presented by rapid changes in grassland creation and management in modern agriculture has enabled it to adjust to massive changes in extent and quality of natural habitat since 1940. It is therefore ironic that changes to goose management in another hemisphere (i.e. the eastern United States) have encouraged the expansion in numbers of *Branta*

canadensis interior that seems to have led to its colonization of West Greenland. This extension of range may now have affected the reproductive success and population size of a similar goose species wintering on the very western fringe of Europe.

No way back?

Although there is no reason to believe that the transition from natural to seminatural and onto more intensive farmland was originally caused by loss of traditional habitats, wetlands, seminatural meadows and salt marshes they have, more recently, been lost in some areas (e.g., Iceland and Norway). Loss may be permanent (through physical destruction of peatlands) or temporary (e.g., changes of grazing regime) although in the latter case, appropriate management measures could restore habitat quality and quantity. In Iceland, almost 100% of intact peatlands had been modified by the late 1990s (Iceland report to Ramsar Convention) and the quality of seminatural meadows and salt marshes in Iceland and Norway have been greatly reduced through cessation of grazing and hay cutting or through drainage. Correspondingly, geese have become highly dependent on farmland habitat, yet have limited opportunity to return to the traditional habitats that they once occupied. The polarization in agriculture because of intensive management of some areas and the abandonment of others (Tombre *et al.*, submitted) further makes geese to concentrate on the most productive crops. In such cases, farmers increase scaring to displace birds from the most susceptible crops, causing serious disruption of feeding time and forcing geese to forage in unsuitable habitats. This has demonstrable costs to fitness measures (e.g., reduced fat scores on departure to the breeding grounds and subsequent decrease in reproductive success and summer survival among followed marked individuals, Madsen, 1994; J. Madsen & M. Klaassen, unpublished results). Hence, during 1998–2003, when intensive scaring was organized in northern Norway, the proportion of juveniles consistently fell below average (10.5%, J. Madsen, unpublished data); the spring scaring is the most likely reason for the recent levelling off in the population or its possible decline.

In northern Europe, generally, marginal agriculture is in steep decline because of the high cost of labour and this is especially evident in Iceland (A. D. Fox *et al.*, unpublished results), where reintroduction of sheep quotas and human resettlement to the city have dramatically reduced grassland management and stock levels since the mid-1980s. Having lured goose populations off their traditional habitats onto productive agricultural land, and having destroyed or modified

much of their traditional habitat, will man now leave the GWFG and the PFG trapped in a migration and wintering strategy shaped by the agricultural activity of the early 21st century? It may well be that as agricultural management declines in northern regions, such landscapes will no longer provide the present levels of nutrient and energy resources to sustain these populations at current levels. If farmland areas of north and west fall into decay as agricultural policies become more rigorous, to what extent will they revert to habitats able to support geese? How successful may geese be in adapting to less productive, postagricultural landscapes as staging habitats, perhaps at lower population levels? On a more positive note, the restricted range and relatively small population sizes involved give some hope for crafting local management solutions if such changes threaten the conservation status of such populations. In particular, the recent focus to further develop agri-environment initiatives as a means of sustaining both human populations and wildlife of the countryside possibly offers a source of support for geese populations not available previously. Organizations in several countries have enough support and finance to farm grasslands specifically for the benefit of geese and other birds, a fact which may be of critical importance in Europe, where enlargement of the European Union necessitates major alterations to farming support programmes in coming years.

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