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The Greenland White-fronted Goose *Anser albifrons flavirostris*

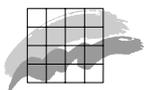
The annual cycle of a migratory herbivore on the
European continental fringe

Doctor's dissertation (DSc)

Anthony D. Fox



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2003

Anthony D. Fox
Department of Coastal Zone Ecology

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Summary

The Greenland White-fronted Goose *Anser albifrons flavirostris* is the most morphologically distinct sub-species of the circumpolar White-fronted Goose *Anser albifrons*. The population breeds in West Greenland and migrates through Iceland to winter in Britain and Ireland. After a period of population decline from the 1950s to the 1970s, protective legislation enacted on the wintering grounds in the early 1980s removed winter hunting as a source of mortality and population size doubled to the present level of 30-35,000, although numbers have fluctuated in very recent years. Declines and extinctions at some wintering resorts continue, despite the nature conservation objective of maintaining the current geographical range of the population. Most research effort has concentrated at the two most important wintering sites, Wexford Slob in southeast Ireland and the island of Islay off southwest Scotland. These two resorts have supported some 60% of the total population in recent years. Irish wintering geese tend to stage in western Iceland and breed in the north of the range in Greenland, whilst Scottish birds tend to use the southern lowlands of Iceland and breed further south.

Greenland White-fronted Geese habitually feed throughout the annual life cycle on the lower stem of the common cotton grass *Eriophorum angustifolium*, which they extract from soft substrates in peatland ecosystems. The restricted extent of patterned boglands (which formed the traditional winter habitat) would undoubtedly have constrained population size, even in a landscape unchanged by Man's activities. Exploitation of this highly specific food in a restricted habitat is also likely to have shaped its highly site-faithful habit and influenced the evolution of the unusually prolonged parent-offspring relationships which distinguishes this population from most other geese. During the last 60 years, the race has increasingly shifted from feeding on natural vegetation habitats to intensively managed agricultural grasslands, which in some areas has brought the population into conflict with agriculture. Despite this change in habitat use, there has been no range expansion, since new feeding traditions continue to be associated with use of long established night time roost sites.

Consistent with providing advice to support the most effective conservation management for the population, the broad aim of the analysis presented here is to begin to identify factors that could potentially limit this population or regulate the rate of change in its numbers. Given that geese are such social animals, it is especially interesting to examine how individual behaviour could influence survival and reproduction, and how this scales up to changes in the overall population.

This thesis therefore examines the annual life cycle of the Greenland White-fronted Goose, concentrating on periods of nutritional and energetic need (e.g. migration, reproduction and wing feather moult) and the way in which individuals may balance their short and longer-term budgets. Body mass and field assessments of fat stores were used as relative measures of body condition (taken to represent the ability of an individual to meet its present and future needs). Greenland White-fronted Geese maintained body mass through mid winter but accumulated mass increasingly until mid April when they depart for Iceland. Assuming 80-90% of this accumulation is fat, departing geese had more than enough fuel from such energy stores to sustain this spring flight. The majority of this mass was depleted en route to Iceland where they staged for another c.15 days prior to the journey onwards to Greenland. Here, geese increased body mass by 25-30 grams per day. In total, this is slightly less than that during December-April but accumulated over a considerably shorter period. Most Greenland White-fronted Geese attained these high rates of mass accumulation on artificially managed hayfields although they fed also on adjacent wetlands. The three most common grass species exploited showed differences in profitability because of differing leaf densities, growth rates and nutrient quality - all of which affected food intake rates and hence the rate of accumulation of stores by geese. Behavioural dominance is a major determinant of access to best food resources in this population. Since individual geese showed different levels of feeding specialisation on the three grass species there is the potential for density effects and social status to influence rates of nutrient acquisition in Iceland that could affect their future fitness.

Arrival mass in West Greenland confirmed that geese lost more mass flying from Iceland to Greenland than during the same flight distance from Iceland to Ireland. The difference was consistent with the predicted extra costs required to cross over the Greenland Ice Cap. After arrival, breeding geese fed intensively for a period of 10-14 days during which mass accumulation for investment in reproduction occurred at the same rapid rate as in Iceland. Female geese protected by attendant ganders were able to exploit a rich food supply (storage organs of plants) during uninterrupted periods of foraging. Nest densities were low and nest habitat apparently unlimited, so it seems unlikely that breeding habitat *per se* limits breeding numbers. More likely, the extent and availability of pre-nesting feeding habitats in the central part of breeding range could limit pre-nesting accumulation of stores. This would potentially limit the numbers of individual females attaining adequate body stores to achieve successful reproduction. Hence, increasing goose densities exploiting a finite pre-nesting food resource may increasingly limit the numbers of geese attaining a level of body condition sufficient to enable successful reproduction. Birds breeding in the north of the summer range stage further south in Greenland (where they compete for resources with locally nesting birds) before moving north. Global climate change models predict that the northern breeding element of the population will face continuing reductions in summer temperature. In addition, northern breeding birds will encounter greater goose densities in southern spring areas with which they must compete for spring food resources.

Despite the recent increase in total population size under protection, the absolute numbers of successfully breeding pairs returning with young to the two most important wintering areas have been more or less constant. This suggests that some finite resource limitation may now operate (most likely on the breeding grounds), restricting recruitment. Amongst known age marked individuals, the probability of survival to successful breeding had fallen from 15% amongst goslings hatched in 1983 to 3% amongst those from 1992 and the mean age of first breeding increased from c.3 years prior to 1988 to c.5 years of age in subsequent cohorts. The proportion of potentially breeding adults returning with young to the wintering areas is falling at both the wintering sites at Wexford and Islay, but the faster rate of decline at Wexford has had a greater effect and is now

causing a decline in wintering numbers there. It may be that the cooling of the climate in North West Greenland and increasing densities further south are already affecting the Wexford wintering birds. At the same time, the Islay wintering birds that tend to nest further south, benefit from improvements in spring climate conditions in central west Greenland.

Greenland White-fronted Geese moult flight feathers at amongst the lowest levels of body mass and showed no change with moult stage, suggesting they meet energetic and nutrient demands from exogenous sources. However, confinement of the flightless geese to the proximity of water to escape predation constrains total available habitat. Newly colonising Canada Geese have increasingly exploited the same moult sites and are behaviourally dominant over Whitefronts. Dramatic increases in the numbers of Canada Geese (which winter in North America) suggest the potential for increasing conflict on the breeding areas between the two species in future.

The increase in numbers since protection from winter hunting at Wexford is consistent with a constant apparent annual adult survival since the 1960s but the relative stable numbers before 1982 seem to have been maintained by the balance between hunting kill and breeding success. Immediately following protection (i.e. in the absence of apparently additive hunting mortality), numbers increased at rates regulated by the potential of reproduction to replace lost individuals. Since the early 1990s, Wexford numbers have declined due to falling fecundity and to a catastrophic loss of first-year birds and their parent adults in one single year. Hence, reductions in reproductive output now seem to be limiting Wexford numbers. Since fecundity has also declined on Islay and some other winter resorts, this appears to be a general phenomenon in the population as a whole at this time. On Islay, reductions in the reproduction rate have yet to halt the linear increase in numbers since protection.

It would therefore appear that the population was limited prior to the 1980s by hunting mortality. Under protective legislation, the population expanded to reach a new equilibrium level set by limits to reproduction. Given the predicted effects global climate change, the increases in goose density and the colonisation of the breeding areas by Canada Geese, the future conditions affecting

Greenland White-fronted Geese are unlikely to remain as they are now. The results of many years monitoring are reviewed in the light of the con-

servation issues facing this population in the future and recommendations are made for future research.

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Dansk resumé

Den grønlandske blisgås *Anser albifrons flavirostris* yngler i Vestgrønland og trækker via Island til overvintringsområder i Storbritannien og Irland. Siden jagtfredningen i vinterkvartererne i 1980'erne er bestanden steget fra 14,300-16,600 i 1970'erne til mellem 30,000 og 35,000 individer i dag. Nogle vinterflokke viser fortsat tilbagegang eller uddør selv om det er et forvaltningsformål at opretholde bestandens nuværende geografiske udbredelse. Knap 60% af bestanden overvintrer på de to vigtigste overvintringsområder, Wexford Slobs i det sydøstlige Irland og Islay i det sydvestlige Skotland. Størstedelen af fuglene fra den nordlige del af yngleområdet overvintrer i Irland og trækker via Vestisland, mens skotsk-overvintrende fugle viser tendenser til at yngle i de sydlige regioner af Vestgrønland og bruge Sydisland under trækket.

Oprindeligt har den grønlandske blisgås udnyttet naturlige vådområdehabitater hvor de igennem årscyklus fouragerede på stænglerne af smalbladet kæruld *Eriophorum angustifolium*. Før den menneskelige påvirkning af deres vinterhabitater begrænsedes bestandens størrelse af udbredelsen af uspolerede moser. Udnyttelsen af den specielle fødekilde i en begrænset habitat har sandsynligvis været årsag til udvikling af stedtrofasthed og forlænget forældre-afkom forhold som er karakteristisk for underarten.

I den anden halvdel af det 20. århundrede har de grønlandske blisgæs skiftet fra naturlige vådområder til kulturgræsenge. Især på Islay er der opstået konflikt med landbrugsinteresser fordi gæssene forårsager markskader. På trods af ændringen i habitatvalg er underarten forblevet meget traditionsbundet i valg af overvintringspladser idet nye fødevaner generelt er bundet til de traditionelle overnatningspladser, og gæssene spreder sig ikke til nye områder.

Formålet med denne afhandling er at identificere faktorer som potentielt begrænser bestandens størrelse og regulerer raten i dens udvikling, og dermed understøtte den mest effektive beskyttelse og forvaltning af underarten i forhold til internationale aftaler om forvaltning af fuglebestande og deres levesteder. I kraft af at gæssene er sociale, floklevende fugle, er det specielt interessant at belyse hvordan individuel adfærd påvirker overlevelse og reproduktion på individ- og bestandsniveau.

Denne afhandling belyser årscyklus hos den grønlandske blisgås med fokus på perioder med særlige nærings- og energibehov (bl.a. træk, reproduktion og svingsfjerfældning) og måder hvorpå individer balancerer deres korttids- og langtidsbudgetter. Kropsvægt og en visuel vurdering af fedtlag er anvendt som mål for kropskondition.

Grønlandske blisgæs opretholder deres kropsvægt igennem vinteren, men viste stigende vægt fra midt af december indtil afrejse til Island i midten i april. Under antagelse af at 80-90% af denne opbygning af depoter består af fedt, har gæssene rigeligt med brændstof til at gennemføre forårstrækket til Island alene på depoterne. Hovedparten af depoterne er brugt op ved ankomsten til Island hvor de opholder sig i ca. 15 dage før trækket videre til Grønland. I Island forøger de deres kropsvægt med 25-30 gram pr. dag. Sammenlagt er dette en smule mindre end for perioden december-april, men er akkumuleret over en meget kortere periode. De fleste gæs opnår disse højere rater af kropsvægtforøgelse ved at søge føde på kulturgræsarealer som anvendes til høslæt, suppleret med fødesøgning i naturlige vådområder. De tre mest udnyttede græsarter udviser forskelle i profitabilitet i form af forskelle i bladtætheder, vækstrater og næringskvalitet. Disse faktorer påvirker gæssenes fødeindtagsrater og dermed tilvæksten i kropsvægt. Hos grønlandsk blisgås er adfærdsmæssig dominans er en vigtig faktor som sikrer adgang til de bedste fødekilder. Fordi individuelle gæs viser forskellige niveauer af fødespecialisering på de tre græsarter kan tæthedseffekter og den socialt betingede dominans af adgang til fødekilderne påvirke indtagsraterne under opholdet i Island, hvilket i sidste ende kan få fitnesskonsekvenser.

Kropsvægten ved ankomst i Vestgrønland viser at gæssene taber mere vægt ved at flyve fra Island til Vestgrønland end på den samme distance fra Irland til Island. Forskellen svarer til den estimerede ekstra omkostning der er forbundet ved at flyve over den grønlandske indlandsis. Efter ankomst fouragerer gæssene intensivt i 10-14 dage for at ombygge energi- og næringsreserver til æglægning. Vægtforøgelsen sker med samme høje rate som i Island. Hunnen, som beskyttes af en agtpågivende mage, søger føde på energirige underjordiske planteorganer.

Redestederne ligger i nærheden af moser med smalbladet kæruld. Redetætheden er lav, og redehabitaten forekommer ubegrænset. Derfor forekommer det usandsynligt, at ynglehabitaten begrænser den ynglende bestand. Derimod er den tilgængelige fourageringshabitat forud for æglægning i det centrale Vestgrønland begrænset og kan påvirke gæssenes tilvækst af energi- og næringsreserver. Stigende tætheder af gæs, som udnytter de begrænsede føderessourcer, kan potentielt begrænse antallet af hunner, som kan opnå tilstrækkelig kropskondition til at gennemføre reproduktionen med succes. Fugle, som yngler i Nordvestgrønland, gør ophold i det centrale Vestgrønland på vejen til deres ynglepladser og oplever konkurrence med lokale ynglefugle. Modeller for klimaforandring forudsiger, at der vil ske en afkøling af forårs- og sommertemperaturerne i Nordvestgrønland, mens der vil ske en opvarmning af det centrale Vestgrønland. Således kan det forudsiges, at de nordlige ynglefugle vil møde endnu flere gæs på vejen nordpå og dårligere klimatiske forhold på deres ynglepladser.

På trods af stigningen i bestandsstørrelsen, som er sket siden jagtfredningen i 1982, har det totale antal af succesfulde ynglepar, der returnerer med afkom til de to vigtigste overvintringsområder, været stabilt. Det antyder, at en ressource - mest sandsynligt på ynglepladserne - nu begrænser rekrutteringen blandt mærkede fugle med kendt alder er sandsynligheden for at overleve frem til succesrig reproduktion faldet fra 15% hos unger klækket i 1983 til 3% blandt unger klækket i 1992. Den gennemsnitlige alder ved ynglestart steg fra ca. 3 år før 1988 til ca. 5 år i efterfølgende kohorter. Andelen af yngledygtige fugle, som returnerede med unger til overvintringsområdet, er faldende ved både Wexford og på Islay, men hurtigst ved førstnævnte, hvilket nu forårsager et fald i det samlede antal, som overvintrer der. Muligvis påvirker afkølingen af klimaet i Nordvestgrønland og den øgede tæthed af fugle længere mod syd allerede nu Wexford-fuglene negativt, mens Islay-fuglene drager fordel af forbedrede klimatiske forhold i det centrale Vestgrønland.

Grønlandske Blisgæs fælder deres svingfjer uden ændring af kropsvægt, hvilket antyder at de kan opretholde deres nærings- og energibudgetter på exogene ressourcer. På grund af prædationsrisiko fra Polarræv er gæssene tvunget til at opholde

sig i nærheden af vand, hvortil de kan flygte. Deres habitat er således af begrænset udbredelse. Canadagæs, som er under indvandring i Vestgrønland udnytter i stigende grad samme fældningshabitat og er adfærdsmæssigt dominante i forhold til grønlandsk Blisgås. Der sker i disse år en dramatisk stigning i antallet af Canadagæs (som overvintrer i Nordamerika), hvilket sandsynligvis vil medføre en forøget konkurrence mellem de to arter.

Stigningen i bestandsstørrelse siden jagtfredningen ved Wexford kan forklares ud fra en konstant årlig returneringsrate siden 1960'erne. Det relativt stabile antal før 1982 synes at have været opretholdt ved en balance mellem jagtdødelighed og ynglesucces. Umiddelbart efter jagtfredningen (dvs. efter bortfaldet af en tilsyneladende additiv jagtdødelighed) steg antallet med en rate, som var reguleret ud fra ynglepotentialet, som oversteg dødeligheden.

Siden begyndelsen af 1990'erne er antallet af overvintrende fugle ved Wexford faldet som følge af faldende fekunditet og et katastrofalt tab af juvenile fugle og deres forældre i et enkelt år. Reduceret fekunditet ser således ud til nutildags at begrænse antallet af Wexford-fugle. Eftersom fekunditeten også er faldende på Islay og nogle andre overvintringspladser, ser det ud til at være et generelt fænomen i bestanden i disse år. På Islay har reduktionen i fekunditet endnu ikke forhindret den lineære fremgang i antal, som har fundet sted siden jagtfredningen.

Det ser således ud til, at før 1980'erne var bestanden begrænset af jagtdødelighed. Efter jagtfredningen er bestandsstørrelsen steget til et nyt ligevægtsniveau, hvor reproduktionen er begrænsende. Med de forudsagte klimaforandringer, stigningen i tætheden af gæs og Canadagæssenes kolonisering af yngleområderne, er det sandsynligt at miljøforholdene, som vil påvirke bestanden af Grønlandsk Blisgås i fremtiden, vil forandres.

Afhandlingen afsluttets med, at resultaterne af 30 års overvågning evalueres i lyset af de forhold, som kan tænkes at påvirke bestandens status i fremtiden. Der gives anbefalinger til forskning, som kan bidrage til en bedre forståelse af de bagvedliggende processer.

1 Introduction

1.1 Why Greenland White-fronted Geese?

At the time when we first became interested in Greenland White-fronted Geese, it looked as if this race of the circumpolar White-fronted Goose was in trouble. It was one of the few wildfowl species wintering in Britain and Ireland that lacked adequate annual census data to determine the trends in its population size. Such information as existed at that time strongly suggested declines and extinctions at wintering resorts throughout its range, especially in Ireland. Like many migratory waterbirds at the time, it was hunted throughout its entire range. Many features of this little population made it attractive to study: its breeding grounds in west Greenland were hardly known to Europeans, although first details of its breeding biology had been described as long ago as 1950. It was known that some birds at least staged in Iceland, but very little was known about what the geese did there or the biological significance of stopover staging there during migration to and from the breeding grounds. Finally, it was believed that the entire world population wintered in Ireland and western Britain, along the Celtic fringe of the European landmass. Here, its use of boglands and low intensity agricultural land in areas with some of the lowest human population densities on those crowded islands meant that its precise distribution and abundance remained poorly known. Little wonder, therefore, that this race of geese attracted the attention of a dedicated band of students, all naively intent on discovering 'the secret' of its decline. The population had all the ingredients for an exciting investigation – a declining population of birds using remote (and naturally beautiful!) landscapes in a relatively restricted part of the globe! How could anyone *not* be intrigued by the prospect?

1.2 How much more do we know after a period of study?

Twenty years on, we know a great deal more, but we are still very far from an adequate understanding of the ecology of the Greenland White-fronted Goose. We are now more confident that the population breeds exclusively in west Greenland

(MS23, MS24), stages on spring and autumn migration in southern and western Iceland (MS4, MS15, MS16, MS18, MS19, MS25, MS26, MS27) and winters at some 70 regular winter haunts in western Britain and Ireland (MS14, Figure 1.1). It has proved possible, through international co-operation, to co-ordinate an annual census of the population on the wintering grounds and to sample age ratios in order to assess changes in productivity and monitor crude changes in survival. Satellite transmitter devices have been deployed on a sample of birds captured in Ireland to follow the precise timing, staging areas and routes taken by geese on migration to and from the breeding and wintering grounds (MS20). We know a great deal more about the breeding biology and summer ecology of the population thanks to summer expeditions to the breeding grounds in 1979 and 1984 (Fox & Stroud 1981a, MS1, MS2, MS3, MS5, MS24). Based on continuing individual marking programmes, we now have long term monitoring of annual survival rate estimates (MS6, MS10), individual behaviour

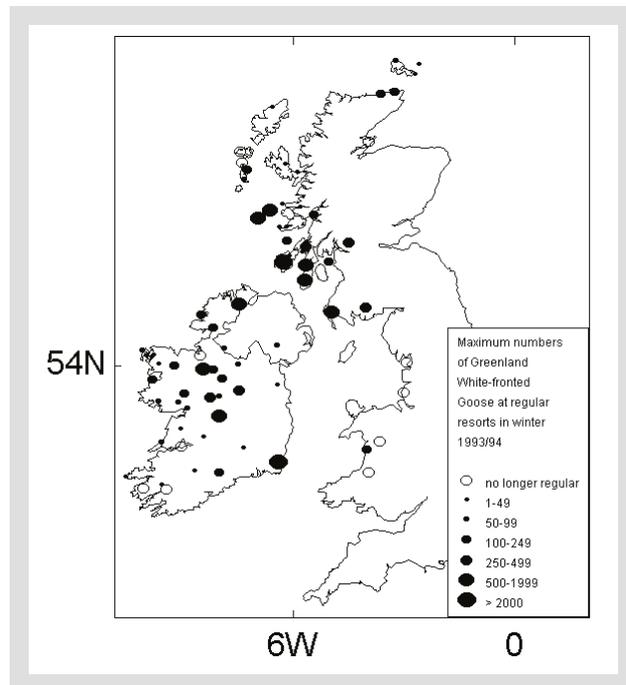


Figure 1.1. Current wintering distribution of Greenland White-fronted Geese in Ireland and Britain (from Fox et al. 1999). Although dating from 1993/94, the distribution has not changed (in terms of the flock size intervals shown on the map) in the interim. Open symbols indicate regular wintering sites currently abandoned (map generated using DMAP).

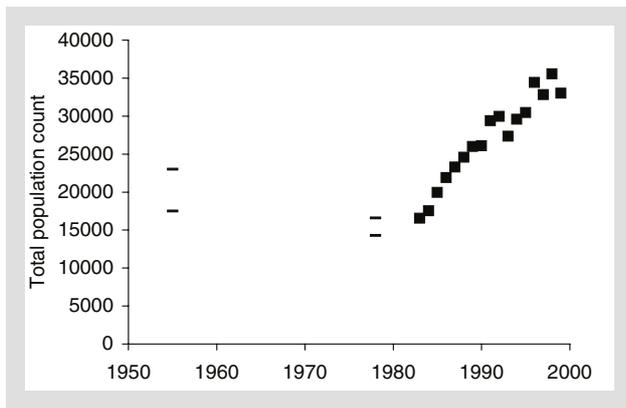


Figure 1.2. Total annual estimated population size of Greenland White-fronted Geese counted during coordinated count coverage on the wintering grounds (from Fox et al. 1999). Counts from the 1950s and late 1970s are upper and lower estimates from Ruttledge & Ogilvie (1979).

(MS7, MS8, MS9, MS11), breeding success (MS8) and plumage characteristics (MS21). On the basis of conservation concern for the population and the availability of new data, a flyway conservation plan was drafted for the population (Stroud 1992), and more recently it was possible to undertake a Population Viability Analysis for that element of the population that winters in Britain (Pettifor et al. 1999).

Based upon the annual census information, the important conservation conclusion from all this research and monitoring activity is that from a population size thought to have fallen as low as 14,000 individuals in the late 1970s, the population now numbers some 33,000-35,000 birds (Figure 1.2). Today, after a period of recovery under protective legislation, the rate of increase in numbers seems for the meantime to be slowing.

1.3 Why this synthesis now?

It could be argued that the job is now done. Indeed, the original imperative for this work (the objective of restoring favourable conservation status to the population) has largely been achieved without seriously enhancing agricultural conflict on the wintering grounds. Surely this is a good time to stop? The following compilation demonstrates why the answer to this question is an emphatic no! White-fronted Geese can live in the wild for 17 years (Cramp & Simmons 1977); hence, we have reached the point in time when the first generation of marked individuals is likely all dead. Only now are we able to start to make ten-

tative statements about patterns of recruitment and survival of cohorts of geese hatched in the 1980s. Only through the sustained maintenance of a marked sample of known age birds in a population such as the Greenland White-fronted Goose is it possible to understand the subtle changes in their long-term population dynamics. This is the problem that faces biologists charged with answering short-term questions relating to long-lived individuals. For this reason alone, it is important to step back and ask the question, how effective has the study of marked individuals in this population been in supplying answers to management questions regarding its long term conservation management?

Population processes are influenced at a range of spatial scales, and the interaction of phenomena that affect populations at these different levels shape overall population change (Wiens 1989, Levin 1992). We are fortunate, in the case of the Greenland White-fronted Goose, that it remains feasible to assess annual population size and reproductive output for a group of individuals that summer over a latitudinal range of 13° (some 1,700 km north to south). Unusually, nowhere throughout this range does the breadth of their distribution exceed 180 km, the maximum breadth of the west Greenland landmass. Since the sub-species breeds typically at low density, there is ample opportunity for differences in local ecological, physical and meteorological conditions to affect local population processes through this long but very narrow range. There are good grounds for believing that there is some segregation of birds of different breeding areas on the wintering grounds, so the scene is set for some interesting comparisons of the behaviour of birds of different nesting provenance. Climate change models predict a general cooling of conditions in west Greenland, especially in the northern part of the breeding range of the Greenland White-fronted Goose (Zöckler & Lysenko 2000). The same models suggest that the summer temperatures of central west Greenland may increase slightly in the short term, such that different changes in the climate may simultaneously affect different elements of the population. Since weather plays a fundamental macro-role in the breeding success of many arctic migratory bird species (Ganter & Boyd 2000), there is a unique opportunity to follow a macro-experiment in the effects of climate change on a whole population. Some of the baseline information offered in the following chapters seem to reflect the first effects of such change.

The Greenland White-fronted Goose is also experiencing inter-specific competition, as expanding numbers of Canada Geese *Branta canadensis* from North America colonise west Greenland, locally displacing the endemic Whitefronts. Wing-moult has been rarely studied as a critical element in the life cycle of the Anatidae, yet it is precisely at this period that competitive interactions between the two goose species are most apparent (Jarrett 1999, Kristiansen 2001). The ecological conditions for breeding White-fronted Geese in west Greenland are therefore most unlikely to remain as they are now, and the existing baseline information will prove invaluable for assessing, and making predictions about, future population change.

Having restored the population to more favourable conservation status of greater numbers and more stable population trends, the future challenge is to maintain this status in the face of greater change and provide solutions to potential conflict. There is a need to integrate the local scale with processes at the macro-scale, to assess local effects and build these into an understanding of overall population change. In particular, since we have evidence that there is some winter/summer segregation, what will be the effects of changes in the summering areas on the winter distribution and abundance of the population? To answer these questions is the challenge for the immediate future. This will require the use of the material presented here to develop a forward strategy for research on this well-described population. Hopefully, such a synthesis would offer a useful model for understanding the effects of complex changes on other migratory bird populations.

Although they are not a major pest to agriculture, there is, nevertheless, local conflict between these geese and farming interests in a few wintering areas, notably in Scotland. Patterns of land-use rarely stand still, and the changes brought about in rural land use on the wintering areas in the last few decades have required that the geese adapt to major modifications of the habitats they have exploited over recent periods and over a longer time span.

Climate change is also likely to be manifest on the staging and wintering areas. Compared with 20 years ago, we now understand a great deal more about the biology and ecology of the population that can assist in developing adequate con-

servation management planning for this singular race of geese.

In this way, we can offer solutions to some of the potential conflicts, and provide informed judgments where predictions would have been impossible a few years ago. More importantly, we can use our knowledge and understanding of this population to make more general inferences about other species and populations. As our understanding of the energetics of migration is continually improved, we can better understand the biological importance of stopover and wintering sites used by these migratory birds and the importance of food quality and quantity, as well as the effects of disturbance, to the overall fitness of individuals. As we understand more about how the behaviour of individuals contributes to their reproductive output and longevity, so we can make more informed predictions about how human activities *affect* these individuals and scale up to the potential *impacts* on the population as a whole.

The responses of individual organisms are not all the same, especially in highly social animals such as Greenland White-fronted Geese, where dominance hierarchies are well established and extended familial relationships shape the individual responses. We need to understand how change affects foraging and reproductive decisions made by individuals, and to translate these local-scale responses through to the impacts at the population level. Such a process is epitomised by the recent development of individual-based behaviour models of the annual cycle of migratory goose populations (Pettifor et al. 2000). Such models require detailed information about critical elements of the annual cycle of the birds, often in widely differing and remote geographical areas at different times of the year. So how do we set about identifying the critical elements and measuring their effects? Greenland White-fronts are long distance migrants, flying perhaps 6000 km in the course of their annual migrations alone, so the factors affecting their reproduction and survival (and ultimately their population size) may be acting in many different ways in different parts of the globe.

1.4 The flyway concept

By definition, migratory waterbirds have evolved life history strategies that enable the exploitation

of a series of habitats separated in space and time. Their mobility offers these organisms the ability to exploit different habitats for different purposes. Alerstam & Högstedt (1982) were the first to suggest that, to survive between reproductive events, birds were exploiting what they termed 'survival habitats' which, for physical or practical reasons (e.g. predation risk), were not suitable for breeding. Equally, 'breeding habitats' (e.g. in arctic areas experiencing extreme weather conditions) were not necessarily available to bird populations between reproduction events. These authors suggested that the relative extent of these two habitats were important factors in determining reproductive and migratory tactics in different bird species. From an evolutionary standpoint, it is therefore important to recognise the role that different habitats have played in shaping the life-history tactics of birds.

In a world increasingly modified by the activities of humans, the availability of both breeding and survival habitats to migratory birds has changed. In some cases, these changes have had a fundamental effect on their distribution and abundance. Loss of wetland habitat has reduced the extent of 'survival habitat' for many species. In contrast, the intensification of agriculture in the 20th Century has greatly increased the quantity and quality of available forage in Western Europe for herbivorous waterfowl. The improved quality of grasslands (through enhanced crude protein content, increased digestibility and extended growing seasons) has undoubtedly increased the carrying capacity of farmed land for avian grazing herbivores (van Eerden et al. 1996). If we are to understand the effects of anthropogenic changes on populations of migratory birds, we need to identify the critical factors that affect their survival and reproductive success and to establish at which points in the life cycle they operate. It seems logical therefore to divide the annual cycle into a series of discrete events, to help identify the specific bottlenecks faced by a waterbird population. In this way, it may be possible to identify factors that either limit the size of that population (i.e. determine some upper level on the number of individuals that can be supported by a specific habitat at a given time) or that regulate the rate of change in the population. The seasonal components may have consequences for survival, reproduction or both and therefore represent critical periods worth intensive investigation to identify causal links between environmental factors and population events. This conceptualisation of

the annual life cycle as a series of seasonal components which highlight the bottlenecks faced by waterfowl populations was developed as the so-called 'Flyway Concept' by the Department of Coastal Zone Ecology, pioneered by Henning Noer and Jesper Madsen. The original aim was to integrate results from individual performance-based studies into a better understanding of how populations function, based on the variation in behaviour of studied individuals, a mechanism now well established in contemporary ecology (e.g. Sutherland 1995). This involved making detailed studies of individual habitat preference and feeding behaviour and relating these to specific fecundity and survival measures of the same individuals in order to understand which factors regulate and limit populations.

Such an approach offers a useful template for use in identifying those processes in time and space that historically have affected the demography of the Greenland White-fronted Goose population over the period for which we have some information, and those that are doing so now. In this way, the life cycle can be broken down into the critical elements, such as spring fattening, migration, breeding, wing-moult, autumn migration and over-winter survival (e.g. Ens et al. 1994). Given that geese are generally long-lived, it is reasonable to expect that relatively small changes in annual adult survival are likely to have a major impact on their population size (e.g. Schmutz et al. 1997, Tombre et al. 1997). On the other hand, the relatively poor reproductive success of *flavirostris*, compared with that of other pan-arctic *Anser albifrons* populations, means that recovery of the population is slow because of low recruitment. The key questions are: what determines natural annual survival? What effect does hunting have on the population? Why is female recruitment into breeding age classes so low? These questions involve the role of spring staging and the accumulation of stores for migration and ultimately for investment in reproduction. What roles do the unusual extended family relationships of *flavirostris* and individual experience play in limiting the proportion of geese of potentially breeding age that return from the breeding areas with young? The challenge has been to determine the role of body condition in individual decision-making concerning migratory tactics, reproduction and survival. For this reason, emphasis is placed here upon changes in body mass and field-derived indices of fat deposits throughout the annual cycle in individuals, as proxies for

more direct measures of 'body condition' in determining factors affecting individual performance.

1.5 The flyway concept as related to Greenland White-fronted Geese and the format of this thesis

The study of the Greenland White-fronted Goose has never been a full time project for any of the characters involved. In Ireland, the National Parks & Wildlife Service has made a substantial annual commitment to research and survey of Greenland White-fronted Geese since the 1960s, when counts and age ratio assessments were made at Wexford. In more recent years, the regular marking of a sample of individuals captured at Wexford and substantial effort invested in the resighting of these individuals has generated an impressive database of knowledge to support the international research and survey effort. However, elsewhere, the work has been carried out on an *ad hoc* basis, gathering data for differing purposes at different stages of the life cycle. The result is something of a ragbag of information, not always well inter-linked, and certainly never based upon a single research plan with well-defined targets and objectives. The available information is therefore scattered, and one purpose of this thesis is to draw together the disparate strands in order to determine what information is available and identify the gaps in the existing knowledge.

Much of the reference material relating to Greenland White-fronted Geese has been gathered in a recent review and need not be repeated here (MS24). This forms the background to the thesis, in the sense that many of the results of studies are summarised there. **Chapter 1** establishes the setting for the thesis. There follows a review of taxonomic relationships and the recent history of the Greenland White-fronted Goose that attempts to conclude something about the potential limits to this population (**chapter 2**). The following chapters explore the elements of the life cycle where critical factors may operate with respect to fecundity or survival. Outside the breeding areas, there are four periods of the annual life cycle when Greenland White-fronted Geese must accumulate stores in anticipation of long migratory flights. The population stops off in Iceland in spring and autumn *en route* to and from Greenland. The geese must accumulate energy stores enough to travel to and from Iceland and Greenland. Since spring

acquisition of stores in anticipation of the spring flight to Iceland, and thence onward to Greenland will also have consequences for reproduction, these two events in the annual life cycle have attracted considerable interest, and have separate chapters to themselves (**chapters 3 and 4**).

On arrival in west Greenland after traversing the Greenland Ice Cap, the geese must again replenish depleted stores in preparation for the reproductive period. Geese were once thought to be largely capital breeders, investing stored nutrients in clutches and their incubation, although this view is increasingly challenged (see review in Meijer & Drent 1999). In the case of the White-fronted Goose, it is now well demonstrated that females indulge in extended periods of pre-nesting feeding when birds can add substantially to their store of nutrients in readiness for egg-laying and incubation (**chapter 5**). For a population in which the reproductive success is well below the average for other populations of the same species, it is important to explore factors that may limit recruitment and reproductive output (**chapter 6**). The period of flight feather moult represents a potentially critical period in annual cycle, since birds become flightless for several weeks, making them more vulnerable to predation and the depletion of local food resources until they regain the power of flight. The duration of moult and the period of pre-migration accumulation of stores in autumn are key elements in the annual cycle of the population (**chapter 7**).

The return flight from Greenland, again stopping off in Iceland, has been little studied, although there remains the potential for occasional mass mortality associated with this migration episode (as well demonstrated for other goose populations, e.g. Owen & Black 1989, Boyd & Sigfusson in press). In comparison with high arctic forms, late summer and autumn are periods of plenty for Greenland Whitefronts, when food in Greenland and Iceland is not especially limiting and the weather is rarely sufficiently severe to cause between year variation in adult annual survival. That said, there remains an autumn hunt of this population, involving some 2,900-3,200 birds shot every year in Iceland. This period remains a priority for future research.

Having reached the overwintering habitat, it is important that this habitat is sufficient in quantity and quality to ensure survival. There was considerable evidence that in the 1950s, habitat

loss caused displacement of geese and over-harvesting was responsible for the decline in the total numbers of Greenland White-fronted Geese. For this reason, it is important to consider how factors operating all year round and variation between and changes within winter habitats may

affect annual survival and immigration/emigration rates on the wintering grounds (**chapter 8**). Finally, a concluding section draws together the disparate strands of the thesis and offers some suggestions for the direction of future research (**chapter 9**).

2 Limits to population size in recent historical times

2.1 Current taxonomic status

The Greater White-fronted Goose *Anser albifrons* is one of the most widely distributed large waterfowl species in the arctic (Ploeger 1968, Ely & Dzubin 1994). Four forms are currently recognised as sub-species around the arctic region (see Figure 2.1 and discussion below).

Coburn (1902) was the first to suggest that the White-fronted Geese in western Ireland more resembled those that wintered in North America than those in Europe. Nevertheless, it was as recently as 1947 that Christopher Dalgety and Peter Scott first described the White-fronted Geese wintering in Ireland, Scotland and Wales as a new race distinct from the European White-fronted Goose *Anser a. albifrons*. The new subspecies they named the Greenland White-fronted Goose *Anser albifrons flavirostris* (Dalgety & Scott 1948). This

form is one morphologically distinct group from the circumpolar distribution, which extends from the central Canadian arctic (west of Hudson Bay) through to Alaska, and from the far east of Russia to the Kanin peninsula (Figure 2.1).

Although there remains considerable discussion about the precise taxonomic relationships, most authorities agree that the breeding range of the nominate race extends from the Kanin peninsula to the Kolyma river in tundra Russia (Cramp & Simmons 1977, Mooij et al. 1999). To the east of this, it is replaced by *frontalis* in Russia, which winters in the eastern Palearctic. This sub-species also breeds across North America and winters in Mexico and along Gulf and Pacific coasts (Ely & Dzubin 1994). However, intensive studies from the Pacific flyway show that allopatric Alaskan breeding groups maintain temporal separation on staging and wintering areas which has probably

contributed to the evolution of previously described phenotypic differences between these populations (Orthmeyer et al. 1995, Ely & Takekawa 1996). These authors suggest that these sub-populations, along with the Tule White-fronted Goose (*A. a. gambelli* which breeds in Cook Inlet, Alaska in the taiga zone and winters in Oregon and California), may represent part of a 'Rassenkreis', a group of subspecies connected by clines. Such a situation is maintained over time through limited but regular genetic exchange between units otherwise segregated in time and space. Hence, the internal genetic uniformity of the existing taxonomic units is unlikely to be as simple as the current sub-species structure might suggest. Nevertheless, in this respect, *flavirostris* remains amongst the most geographically isolated

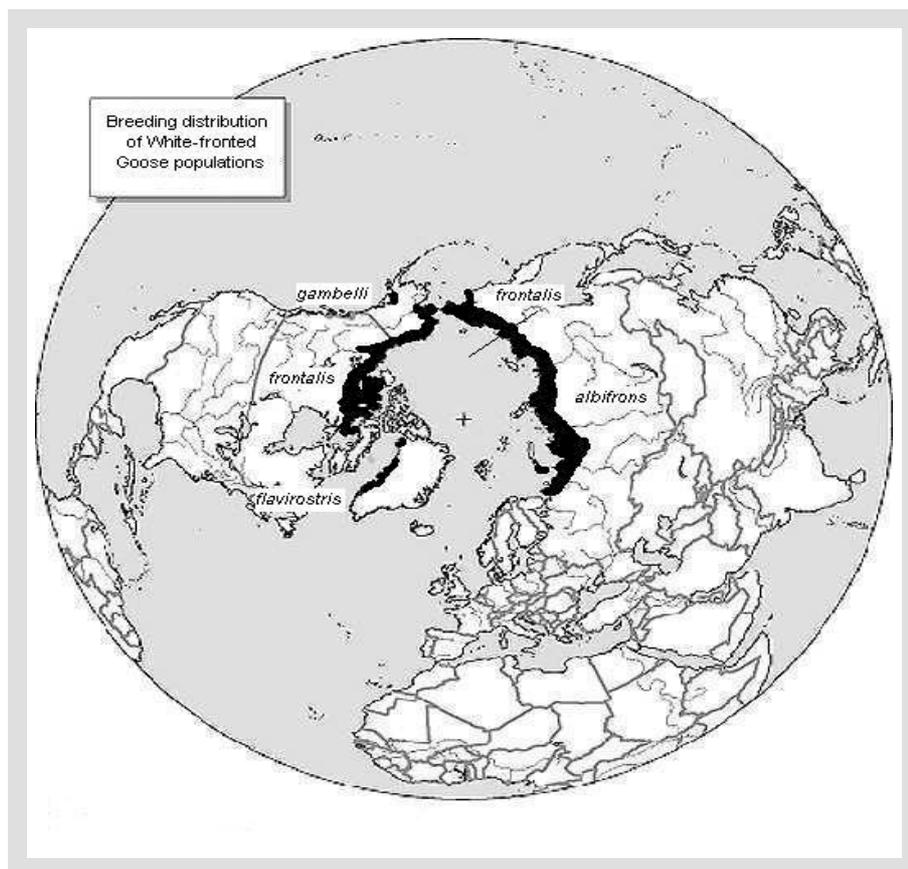


Figure 2.1. Breeding distribution of currently recognised White-fronted Goose subspecies, *flavirostris* (Greenland), *frontalis* (Nearctic and Eastern Palearctic), *gambelli* (Alaska) and *albifrons* (Palearctic), based on Cramp & Simmons (1977) and Ely & Dzubin (1994).

unit of all the forms, a feature that is likely to have maintained a distinct genetic identity, at least in the period since the last glaciation.

2.2 Evolutionary history

Johansen (1956) suggested that White-fronted Geese evolved from the closely related Greylag Geese *Anser anser* that is known from the Pliocene in central Europe (<7 million years before present), whereas the earliest White-fronted Goose remains are only of Pleistocene origin (<2.5 million years B.P.). This has since been confirmed by recent genetic evidence (Ruokonen et al. 2000). This is consistent with the general impression of sister-species separations in avian groups during the Pliocene, whereas the oscillating Pleistocene climatic conditions were more active in phylogeographic separation within species (Avisé & Walker 1998).

It seems likely that towards the end of the Tertiary period, when the arctic climate became substantially colder, White-fronts segregated from the larger ancestral Greylag form, which would have been expected to remain further south in more temperate conditions. From this Old World origin, the White-fronted Goose was able to spread throughout the entire arctic, colonising the New World during the Hoxnian Interglacial (note the British nomenclature for Quaternary periods is used throughout here for consistency: 400,000-367,000 year B.P., Figure 2.1, Fox & Stroud 1981b). The subsequent Wolstonian glacial period (which continued to 128,000 years B.P.) forced these forms south again, probably resulting in the isolation of 'Atlantic' and 'Pacific' forms. During the last interglacial period (the Ipswichian 128,000-60,000 years B.P.), the latter spread widely from refugia in the Bering Sea region in both directions, resulting in the presence of *frontalis* in the eastern Palearctic.

Johansen (1956) suggested that, during the last glacial (the Devensian 60,000-12,000 years B.P.), the nominate race survived in north Siberia refuges. The *frontalis* form persisted in the Beringian Refugium, recolonising North America during the subsequent amelioration and he considered that the ancestral Atlantic form gave rise to *flavirostris*, which survived the last glaciation in the ice-free tundras of western Europe, especially the southern North Sea and Ireland.

Later, Ploeger (1968) offered four different possi-

ble origins for *flavirostris*. (1) He considered that there were morphological similarities between *flavirostris* and *albifrons* that pointed to a common origin, and that the present separation was the result of the use of different refugia in the North Sea area and Siberia respectively. (2) Alternatively, *flavirostris* detached from eastern American White-fronted Geese after their spread across North American tundras in post-glacial times. (3) Another possibility is that *flavirostris* was the eastern element of a pre-Devensian White-fronted Goose population that managed to survive in eastern North America. (4) Finally, he considered *flavirostris* could represent an older population differentiated from other forms at an earlier stage, which spread westwards from Eurasia before the last glacial period.

Of the above, (1) seems the least likely now. Based on various length parameters, *flavirostris* is more different to the nearest *albifrons* (nesting some 3,500 km east in Kanin) than to any other circumpolar *A. albifrons* forms (from tarsus, bill and wing measurements from *A. albifrons* caught through the range, C.R. Ely in litt.). Indeed, based on measurements, *flavirostris* is most like *albifrons* from the Central Canadian arctic (which nests some 1,500 km west) and the sub-arctic *gambelli* of Alaska (C.R. Ely in litt.). If similarity of morphological form can be relied upon in this respect, this suggests that the race is more likely to have originated from easternmost elements of White-fronted Goose populations in North America. Furthermore, during the glacial maximum of the last glacial period, ice extended down to the southern North Sea, joining ice caps that covered Greenland, Iceland and Scandinavia. Despite lowered sea levels, there was never a time when there were land bridges between Greenland and Iceland or between Iceland and North Sea tundra areas. Hence, if Greenland White-fronted Geese had North Sea refugia, at some stage since the height of last ice age, the ancestral stock must have shifted their breeding grounds to Iceland and thence from Iceland to west Greenland. The distances involved in these distributional leaps would have been almost exactly the same as the migratory journeys at the present time. However, there remains considerable debate as to whether there were ice free land areas in west Greenland and Iceland (see Ploeger 1968, Denton & Hughes 1981, and Fig. 12 in Piersma 1994), so it may well be that Greenland White-fronted Geese have been long separated from other stock.

Despite the morphological similarities to support a recent New World origin for *flavirostris*, there is no suggestion of regular wintering grounds for White-fronted Geese in the eastern United States, where *flavirostris* remains a rare vagrant (e.g. Hewitt 1948, Parkes 1960, Finch 1973). At the times of maximum extent of ice cover during recent glacial periods, there were never land bridges between west Greenland and Canada (Andrews 1982). It is also interesting to speculate how ancestral Greenland White-fronted Geese originating in North America came to have a Palearctic migration system like that of the Old World Wheatear *Oenanthe oenanthe* that also breeds in west Greenland but migrates to Iceland to Europe and Africa in autumn.

All of the potential theories relating to origins of *flavirostris* suffer from weaknesses of one type or another, and the available fossil and other evidence simply does not exist to support or refute these ideas. The current distinct feeding ecology and habitat use of *flavirostris*, if long established, would have restricted its distribution. The exploitation of wetlands of a particular maritime type, especially peatland formations, would have restricted the race geographically to its current world range on the mild western fringe of the European landmass. The geographical, morphological, behavioural and demographic characteristics of the sub-species suggest its long separation from other presently existing races, but confirmation will have to await appropriate genetic analysis embracing all the different forms identified within the current *Anser albifrons*. Collaborative analysis is currently well advanced to describe the morphological variation in different population elements (Ely et al. in preparation). This will be the precursor to a major genetic analysis (based upon an existing and growing archive of blood samples gathered from around the arctic) to establish more clearly the phylogeny of this species and its various described sub-species.

2.3 Factors affecting the current distribution

The present wintering distribution of the Greenland White-fronted Goose is concentrated along the northern and western fringes of Britain and Ireland (Fox et al. 1994a, MS14). This distinctive distribution mirrors the climatic template for the formation of oceanic blanket bog. This habitat formed the traditional overwintering habitat for

the subspecies before Man substantially modified the landscapes of Britain and Ireland (Ruttledge & Ogilvie 1979, Fox et al. 1994a).

The Greenland White-fronted Goose specialises on feeding by up-rooting cyperacean species to consume their nutritious lower stem storage organs. In particular, the common cotton grass *Eriophorum angustifolium* was, or is still, eaten by the geese in Scotland, Wales, Ireland, Iceland and Greenland (Ruttledge 1929, Cadman 1953, 1956, 1957, Pollard & Walters-Davies 1968, Madsen & Fox 1981, MS2, MS4, Fox et al. 1990). This species of cotton grass is common throughout Western Europe, but thrives well where high rainfall and a mild wet climate creates patterned blanket and raised mire systems. Oceanic mires characterised by such complex surface topography have well-developed water- and *Sphagnum* moss-filled depressions. Although not necessarily the optimum conditions for the growth of *E. angustifolium*, such wet peatland depressions facilitate the easy extraction of the lower stem parts of the plant favoured by the geese. In contrast, *E. angustifolium* can be vigorous and abundant in more mineral wetland soils, but in such situations, the below-ground plant parts are difficult or impossible to extract by geese.

On the same oligotrophic bogland habitats, the Greenland Whitefront also consumes the White-beaked Sedge *Rhynchospora alba*, which overwinters as small bulbils which are highly nutritious and much sought after by the geese (Cadman 1953, 1956, 1957, Pollard & Walters-Davies 1968).

The Greenland White-fronted Goose is also confined to an area of Britain and Ireland defined by the mean January 3°C isotherm (Belman 1981). The low probability of prolonged ground frost throughout the winter period within this range is thought to be an important factor that permitted the geese to extract the subterranean stem bases of *Eriophorum* and bulbils of *Rhynchospora* from the soft *Sphagnum cuspidatum*, *S. auriculatum* and *S. recurvum* lawns (MS24). This theory is supported to some extent by the fact that at least 4 flocks in Ireland and 1 in Wales became extinct after the severe winter of 1962-63. In that winter, daily sub-zero temperatures occurred continuously in western Britain from 23 December 1962 until 6 February 1963 (Beer 1964). In that period, Greenland White-fronted Geese were displaced when their bogland habitats were frozen, and

birds were picked up dead or dying away from their normal haunts (Ruttledge & Ogilvie 1979, Fox & Stroud 1985). Large numbers of *albifrons* also died of starvation that year, but there was no evidence of range contraction for this population, which is less winter site-loyal and feeds more on agricultural grasslands (Beer & Boyd 1964).

Even where flush runnels and the pool and hummock topography are abundant as surface features, their extent (and therefore the extent of cotton grass and other favoured peatland food species) represents a tiny fraction of the entire bog biotope. Furthermore, by definition, their distribution is highly patchy, so any herbivore exploiting such a resource would be expected to show appropriate behavioural and feeding ecology adaptations. For example, because both *Eriophorum angustifolium* and *Rhynchospora alba* are only locally abundant, foraging could rarely take place in large flocks, since no one area could support more than 10-20 foraging individuals for prolonged periods. The broken topography of blanket and raised mire systems makes approach by potential terrestrial predators (such as Fox *Vulpes vulpes*) relatively simple. Hence, shared vigilance would be expected to favour the cohesion of small groups defending feeding patches rather than lone foraging individuals prepared to risk predation as the costs of gaining access to interference-free foraging opportunities and maintain high intake rates. On the other hand, the locally restricted, patchy but rich food resource would have precluded the development of large flocks typical of other subspecies of *Anser albifrons* exploiting open grass swards.

For the reasons considered above, the subspecies was probably always highly restricted in its wintering distribution. Oceanic mires with conspicuous surface patterning reach their southern limit in Britain and Ireland (Lindsay 1995, Lindsay & Immirzi 1996), and those in Scandinavia to the east and north are frozen in winter rendering the food inaccessible to the geese. In recent centuries, the wintering range is unlikely to have been very different from that today, and the habitat signature that defines their distribution would have always been highly limited in extent, even allowing for widespread loss of boglands as a result of Man's activities in the last 500 years.

Heavy exploitation by Whitefronts may locally remove all *Eriophorum* shoots, and the plant may take a year or more to recover to levels of biomass

prior to goose exploitation (Hupp et al. 2000, MS24). This also has consequences for the way in which a herbivore should exploit the feeding resource, since exploitation of one feeding patch in year t may render this area a poor foraging area in year $t+1$ and perhaps even in $t+2$. Hence some knowledge of the spatial arrangement of this patchy feeding resource and the location of alternative feeding sites (that can be used in successive years) might also favour a social system that involved learning by young members of a group about alternative feeding sites (linked perhaps by a common night-time roost site).

The geographical distribution of the Greenland White-fronted Goose may always have been highly restricted, limited by a rich feeding resource that sustained the geese throughout the winter, the distribution of which was highly patchy, both in time and space. This presumably favoured high site fidelity and the "cultural" accumulation of knowledge as the most effective means of exploiting the bogland biotopes. This in turn resulted in low densities of these specialised herbivores concentrated in relatively small pockets of habitat. If the Greenland White-fronted Goose was confined to bogland habitats in this way, it seems likely that the population would always have been extremely limited in its range and abundance by the nature of its habitat.

2.4 Changes in habitat and abundance in the 20th Century

Given the waterlogged nature of their habitat, and the inaccessibility of many of their winter haunts, the Greenland White-fronted Goose wintering habitats were probably left largely untouched until the mid 19th Century, with many peatland areas unmodified well into the 20th Century. Despite the need for fuel from peatlands, domestic turbaries were unlikely to have extracted peat by hand at a rate that would have threatened the goose habitat. Indeed, there is evidence from at least 5 different Welsh, Islay and west of Ireland wintering sites, that abandoned hand-cut peat diggings perpetuated feeding habitat for Greenland White-fronted Geese, by creating the wet floating *Sphagnum* lawns from which the food plant *Eriophorum* can be most easily extracted (Fox & Stroud 1985). Furthermore, despite the pressure of human densities on the land that resulted in the creation of 'lazy beds' in the most extraordinary situations in the highlands and islands of

Scotland, the wettest peat soils were so infertile and waterlogged as to offer a last refuge for wildlife at that time from a hungry human population. Greenland Whitefronts were described as numerous and widespread throughout the bogs of Ireland (Ussher & Warren 1900), but extensive drainage, started during 1845-1855, was thought to have made the first impact on goose feeding habitat, resulting in many geese being forced to leave their traditional habitats (Ruttledge & Ogilvie 1979).

Seasonally flooded grassland (such as the callows of the Shannon Valley floodplain in Ireland) was probably always of some importance as wintering habitat for Greenland White-fronted Geese (H.J. Wilson in litt.). During the 20th Century, whether because of drainage and destruction of their former natural habitats, or through their discovery of the foraging opportunities offered by low intensity agricultural grassland, Greenland White-fronted Geese increasingly resorted to rough pasture in Ireland and Scotland. Although the geese may still utilise boglands and peat systems for night-time roosts, there are few flocks that continue to feed exclusively on natural habitats throughout the winter (Norriss & Wilson 1993, Fox et al. 1994a, MS14). The increasing use of semi-natural grasslands apparently accelerated in the latter half of the 20th Century, when there was also an increase in the extent and goose use of intensively managed farmland. Although habitat destruction has been cited as the cause of shifts in habitat use of this species (e.g. Ruttledge & Ogilvie 1979), Norriss & Wilson (1993) were strongly of the opinion that the movement from semi-natural grasslands to more intensively managed agricultural land coincided with beneficial changes, rather than losses of traditional habitats. They observed that goose use of reseeded grasslands was typically opportunistic within existing feeding areas, whilst longer established, poorer quality habitats were abandoned. Hence, in terms of responses to new feeding opportunities provided by the dramatic rates of changes in agriculture in the last 50-100 years, the Greenland White-fronted Goose may have shown greater flexibility in adapting to new sources of food than might have been expected.

This adaptability was nowhere more dramatic than in the vicinity of Wexford Harbour in SE Ireland. At the beginning of the 20th Century, the Wexford Slobs were embanked and claimed for agriculture from the intertidal waters of Wexford

Harbour. Whitefronts began using the newly created large fields of rough grassland of the area, so that by 1925, this was already the most important Irish wintering site as it remains to the present (Kennedy et al. 1954, MS14).

In Britain, the compilation of a historical picture of the distribution and abundance of Greenland White-fronted Geese in winter was complicated by the occurrence of European White-fronted Geese *A. a. albifrons* from Russian breeding areas (which do not occur in Ireland). Since the subspecies was only defined in 1948, it is not possible to determine the breeding origins of White-fronted Goose wintering groups with certainty before that time. The White-fronted Goose was to be found in the late 19th and early 20th Century in nearly all the haunts where *flavirostris* occurs today (Berry 1939, Ruttledge & Ogilvie 1979). This included Islay, identified as the principal haunt for the species as long ago as 1892, supporting "large flocks", as well as Tiree, Coll and Jura (Harvie-Browne & Buckley 1892). The species has certainly been long established in Caithness and Orkney (Harvie-Browne & Buckley 1887, 1891). The only notable change appeared to be on the Outer Hebrides, where the species was considered rare until the late 1800s when it was reported in markedly increasing numbers (Harvie-Browne & Buckley 1888, Berry 1939). However, large numbers have probably always passed over the Western Isles on passage in spring and autumn, when large numbers may temporarily also land, so their fluctuating fortunes may have more to do with the interpretation of such patterns than any dramatic change in over-wintering abundance. Wintering flocks of White-fronted Geese were also known in the 19th and early 20th Centuries from North Wales (Fox & Stroud 1985), Lancashire and Westmoreland. All were associated with inundated wetlands or former peatland areas. It is highly probable, based on their reported habitat use, that most of these would have been Greenland birds.

As in Ireland, the use of traditional bogland habitats for daytime feeding has become increasingly rare amongst British-wintering flocks, as geese forage increasingly on grasslands. The major concentrations on Islay and Kintyre increasingly exploit intensively managed agricultural grasslands, even though they supplement their diet by feeding on bogland roosts at night (MS24). Even in Caithness, where geese still fed by day on the Flow Country patterned mire peatlands until the

1970s, all are now confined by day to agricultural habitats (MS24).

In 1960, Major Robin Ruttledge became aware that numbers of Greenland White-fronted Geese had been decreasing in Ireland over at least a decade and he issued a circular to contacts in an attempt to determine if this was widely the case. The results of his survey and extensive correspondence confirmed his suspicions that numbers had declined throughout the range and some former haunts were deserted (Ruttledge 1973). By contrast, at the same time, apart from the desertion of one important Welsh site, Cors Caron (not connected with habitat change, Fox & Stroud 1985), rather little change was taking place amongst the known flocks residing in Britain. Major Ruttledge and Malcolm Ogilvie began to compile the historical information available relating to wintering Greenland White-fronted Geese and they published their findings (Ruttledge & Ogilvie 1979).

The historical evidence for changes in the size of the Greenland White-fronted Goose population is relatively limited, since prior to the 1940s, information is scant and anecdotal. Although the Wildfowl Trust had pioneered the development of count networks and research programmes into most wintering goose populations in Britain during the 1950s, the Greenland Whitefront, with its remote wintering resorts and highly dispersed nature was far less known. Hugh Boyd established regular counts on Islay in the 1960s and sampled the proportion of young birds in each winter there. Malcolm Ogilvie continued this annual count during his counts of Islay-wintering Barnacle Geese *Branta leucopsis* from the Greenland population. In the mid-1950s, Boyd (1958) analysed the ringing/recovery data generated by the capture programme initiated in Greenland by Finn Salomonsen at the Zoological Museum in Copenhagen. At Wexford, Oscar Merne established regular counts of the Whitefronts in the late 1960s, incorporating an assessment of the proportions of young in the flocks.

Information before these efforts was very scanty. Berry (1939) and Baxter & Rintoul (1953) were the first to attempt a summary of the status of the White-fronted Goose based on available information, but this did not enable an assessment of overall abundance. Atkinson-Willes (1963) suggested British wintering numbers during 1946-1961 to be 2,500-4,500 and Ruttledge & Hall Watt (1958)

estimated 8,850-11,200 in Ireland during 1946-1956. However, Ruttledge & Ogilvie (1979) reviewing additional information available following that time suggested totals of 4,800-5,800 in Britain and 12,700-17,300 in Ireland in the 1950s. They carried out the first full collation of available information and concluded that the global population had declined from 17,500-23,000 at that time to 14,300-16,600 in the late 1970s, which they attributed largely to loss of habitat (especially loss of bogland habitats in Ireland), shooting and disturbance. They considered that the Irish wintering numbers had declined by 50% from the 1950s to the 1970s despite stable numbers at the most important site Wexford Slobs. This included the desertion of at least 29 sites and declines at a further 33. During the same period, the British population had actually increased overall by c.13%, especially in Scotland, although 2 flock extinctions of 100 (Morecambe Bay, England) and 450 (Cors Caron, Wales) and 3 flock declines were noted. The net loss of 7,000 geese from Ireland was not, however, balanced by the gains in Scotland (c. 2,000 birds, Ruttledge & Ogilvie 1979).

Thorough as the survey of Ruttledge & Ogilvie (1979) was, these authors missed a very small number of flocks, especially in remote Scottish sites. Hence, subsequent survey has indicated a modest increase in the number of traditional flocks over those that they reported.

The reasons for the extinctions and declines were inevitably site specific, the majority of the changes at Irish sites being ascribed to afforestation, drainage or (in some cases) complete removal of peatlands as a source of fuel (Ruttledge & Ogilvie 1979). At some sites, the same authors also cited shooting and hunting disturbance as contributory factors. By the late 1970s, it had become clear that there was an urgent need for information relating to the status and distribution of the subspecies on its wintering grounds in order to fully determine the conservation needs of the population (Owen 1978).

The decline of the wintering flock of Greenland White-fronted Geese wintering on the Dyfi estuary in central Wales attracted the attention of a group of students who started to undertake research and established the Greenland White-fronted Goose Study (GWGS) in the late 1970s. This group set up a regular count network at all known sites in Britain. Its further aim was to study and obtain further information about all aspects

of this goose population. At the same time, the pioneering work of Major Ruttledge laid the basis for the establishment of a network of counters in Ireland, co-ordinated by John Wilson and Dave Norriss of the Irish Forest and Wildlife Service (latterly the National Parks and Wildlife, Dúchas, The Heritage Service). The network comprises mostly Conservation Rangers supplemented with BirdWatch Ireland volunteers and collates habitat, disturbance, production data as well as organising the counts. These counts aimed to provide an assessment of numbers at all known wintering sites at least twice a year (generally monthly throughout the season where possible) with a measure of breeding success based on a sample of the proportion of young birds of the year. This system has now been operating annually since 1982/83 and generates annual population estimates and assessment of breeding success (Fox et al. 1994a, MS14).

2.5 Changes in distribution and abundance since protection in 1982/83

Before 1981, the Greenland White-fronted Goose was legal quarry throughout its entire range. There is little doubt that during 1950-1970, the population was suffering damaging effects of habitat loss and modification on the population as well as a considerable off-take that occurred through hunting. Birds were being captured and killed on the breeding areas, shot legally in Iceland in autumn, as well as poached illegally there in spring. Substantial numbers were shot on the wintering areas, particularly in Ireland (where this was one of the few wild goose species widely available as a quarry species).

Following the first appraisal of the global distribution and abundance of the population in the 1970s, conservation concern was expressed for the Greenland White-fronted Goose, particularly because of the decline in numbers in Ireland during the 1950s-1970s (Owen 1978, Ruttledge & Ogilvie 1979). As a relatively long-lived bird, the Greenland White-fronted Goose is sensitive to even small scale changes in annual adult survival. Limitation of the hunting kill was an obvious management response to attempt to restore the population to a more favourable conservation status. Hence, the conservation status of the subspecies was modified throughout its range, especially through protection from hunting, and in latter years, through site safeguard programmes (see

Stroud 1992 for full details of protection measures). In summary, the population ceased to be legal quarry in Ireland and Scotland from 1982 (although this moratorium was lifted at Wexford in the winters of 1985/86 and 1989/90 under strict bag limitation) and in Northern Ireland in 1985. The species has been protected at its only remaining regular wintering site in Wales, the Dyfi Estuary, by a voluntary shooting ban in place since 1972 (Fox & Stroud 1985). In Iceland, the species remains legal quarry in autumn where 2,900-3,200 geese have been shot each year (Wildlife Management Institute 1999). There has been no significant trend in the proportion of marked birds recovered in Iceland annually since 1984 ($F_{15} = 0.11$, $P = 0.74$), suggesting a constant proportion have been shot over this period (mean $3.8\% \pm 0.40$ SE marked birds shot and reported in Iceland per annum). Since 1985, the population remains legal quarry in Greenland only during 15 August – 30 April, extending the protection in the nesting season to spring migration as well. It is thought that currently some 100-200 geese are shot there annually (MS24).

Given the high site fidelity shown by the species on the breeding, wintering and staging grounds (MS5, MS7, MS9, MS27), site safeguard is clearly an important element in any nature conservation strategy to maintain key areas and hence maintain the existing size of the population (Stroud 1992). Use of the Ramsar 1% criterion for site protection has proved an effective mechanism to focus conservation priorities on the larger concentrations, but fails to protect the sites used by the smaller more vulnerable flocks that show the most dramatic declines (MS14). Nevertheless, site protection in the UK (through EEC Birds Directive SPAs, Ramsar Wetlands of International Importance, National Nature Reserves (NNRs) and Sites of Special Scientific Interest (or in Northern Ireland - Areas of Special Scientific Interest (ASSIs) cover, in whole or in part, habitats used by geese at 22 sites. The UK SPA network is anticipated to support at least 8,000 geese at 12 SPAs specifically classified for Greenland Whitefronts (an estimated 59% of the British total and 28% of the international population in the mid-1990s; Stroud et al. in prep.). The SPAs include a state-owned NNR, Eilean na Muice Dubh/Duich Moss on Islay, the most important single roost site in the UK. This was acquired following the threat of commercial peat cutting in the 1980s (Stroud 1985; Nature Conservancy Council 1985; Greenland White-fronted Goose Study 1986). Statutory pro-

tection measures are supplemented by nature reserves established by non-government organisations, such as the Royal Society for the Protection of Birds (five reserves - on Islay, Colonsay, Coll, Loch Ken and the Dyfi Estuary).

In the Republic of Ireland, site protection is now founded upon designation of internationally important sites and Natural Heritage Areas (NHAs, formerly Areas of Scientific Interest ASIs). Fifteen actual or proposed SPAs and/or Ramsar sites, 31 NHAs and 4 additional areas covered by management agreements in Ireland protect areas used by all but 5 of the regularly wintering Greenland White-fronted Goose flocks. However, the extent of site-protection is less than the total area used at some localities.

In Iceland, there is only one site with formal protection used by Greenland White-fronted Geese, but the most important staging area, Hvanneyri Agricultural College in the west of Iceland, is currently being negotiated as a potential reserve. The current voluntary ban on shooting at this one site has made this the single most important staging area in Iceland, with up to 1,600 geese staging in spring and probably more in autumn.

In Greenland, the Home Rule Authority announced the declaration of five major Ramsar wetlands of international importance in 1989, covering some 700,000 hectares of the goose summering areas (see Jones 1993 and Fox et al. 1994a for full details). Based on aerial survey in 1992, it was judged that the protected areas north of Kangerlussuaq (including Eqalummiut Nunaat), Naternaq, and three important areas on Disko Island: Aqajarua-Sullosuaq, Qinguata-Kuussuaq and Kuannersuit kuussuat together hold approximately one fifth of the summering population. The very important wetlands of the Svartenhuk Peninsula have also been considered for future designation as a Ramsar site.

With the provision of such site safeguard measures, the population has clearly seen a recent halt in the serious losses of habitat that it experienced during the 19th and 20th Centuries. Nevertheless, throughout the wintering areas, nature conservation protection has concentrated upon protection of the most important natural and semi-natural habitats, as well as safe roost sites that have been used for many years. Rarely do site management plans include specific measures to maintain and enhance habitat quality and quantity specifically

for the geese. Since Greenland White-fronted Geese have increasingly shifted to feeding on agricultural land on the wintering areas where the feeding habitat is not in anyway safeguarded, 'wider countryside' conservation measures in these agricultural areas may be appropriate to support site safeguard of roosts in some situations. In these circumstances, especially in the Republic of Ireland, local management agreements have been adopted to maintain local agricultural conditions suitable for geese. Only in relative few situations in Ireland have land acquisitions by the state resulted in major reserves specifically for White-fronted Geese. This is the case at Wexford Slob Wildfowl Reserve in SE Ireland, where 470 ha of farmland have been acquired primarily for feeding and protecting Greenland White-fronted Geese during the winter and providing increased public awareness through visitor observation and interpretation facilities (Wilson 1996). There also remains considerable scope for improving site safeguard measures in Iceland.

Following protection from hunting on the wintering range in 1982/83, the population increased from 16,500 in 1983 to 33,000 in 1999, although the rate of increase has slowed in recent years. The population increased at the rate of 6.6% per annum until 1991/92, since when total numbers have varied between 30,000 and 35,000, dependent largely upon changes in breeding success. The most dramatic increases were evident at the two most important wintering resorts. At Wexford, peak winter counts increased from 6,300 in 1982/83 to 8,500 in 1999/2000 (after a maximum of 11,000 was reached in 1988/89) and Islay from 3,900 to 13,800 (after a peak of 15,400 in 1995/96 see Figure 2.2). One feature that makes *flavirostris* of special interest is that different wintering groups show very different patterns of population change, despite the overall increase in numbers. Wintering numbers on Islay have shown a linear increase under protection, whilst those at Wexford have decreased in recent years after an initial period of increase (Figure 2.2, MS14). Other flocks have shown less dramatic increases; from regular counts at eight wintering sites in years before and after protection, five sites showed no trend before protection and significant increases afterwards, two stabilised after protection and one showed increasing trends before and after protection (MS14). Seven flocks became extinct during 1982-1995, 35 showed no significant trends and 20 showed increases (MS14). Despite all the conservation activity, therefore, some flocks con-

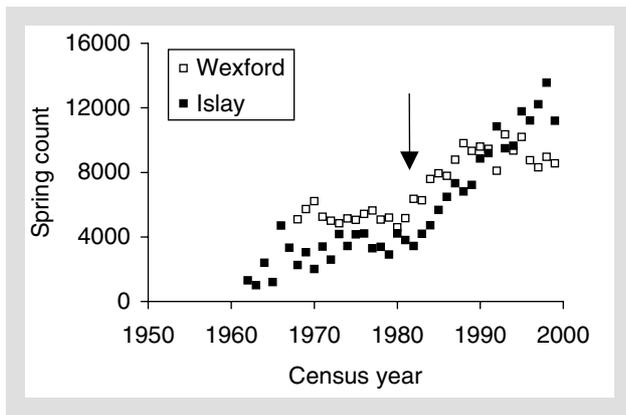


Figure 2.2. Annual spring counts of Greenland White-fronted Geese at the two most important wintering sites, Islay in the Inner Hebrides of Scotland and Wexford Slob in south-east Ireland. The vertical arrow indicates protection from hunting at both sites.

tinue to decline in number or disappear, a process which is not matched by colonisation of new wintering sites, only one of which, in eastern Ireland, seems to have become regular.

2.6 What of the future for the Greenland White-fronted Goose?

The conservation of a relatively small population of one race of an abundant circumpolar species is not a high priority in its own right. Nevertheless, the Greenland White-fronted Goose became a “flagship” organism for the conservation of peatlands on its wintering grounds during the 1980s, representing a top consumer organism of fragile peatland systems under threat from forestry, commercial peat exploitation and drainage at that time. Even in areas where they no longer feed on peatlands, the geese exploit features of an extreme oceanic low intensity pastoral system that supports a rich ecologically diverse community (Bignal et al. 1988, Bignal & McCracken 1996). Conservation actions to protect Greenland White-fronts in winter therefore safeguard a set of unusual and scarce habitats that also support other breeding and wintering species. The research and conservation effort invested in the population over the years now provides a long time series of annual numbers, distribution and breeding success amongst a discrete population of migratory waterbirds. The marking programme, started in Greenland in 1979 and continued to the present (largely in Ireland where birds continue to be collared on a regular basis), provides a 20 year record of individual life histories. In the fullness of time

(since these geese are long lived), these records will provide important additional insights on changes in such critical parameters such as age of first breeding, lifetime reproductive success and mortality. The very process of studying this population has given the Greenland White-fronted Goose scientific interest which may offer some insights into population processes and conservation strategies to protect other taxa.

The Greenland White-fronted Goose also faces new and different challenges in the immediate future. Global climate change has the potential to modify the meteorological conditions of the bird throughout its range, and hence the habitats and phenology of growth of plants which they exploit. Nowhere is this more of a potential threat than on the breeding areas, where change is forecast to be most dramatic. Model predictions agree that north-west Greenland will experience cooler summers and therefore increasingly delayed springs (Zöckler & Lysenko 2000) and there are indications that these patterns are already evident (Rigor et al. 2000). As is discussed in depth elsewhere in the thesis, there is mounting evidence for ‘leap-frog’ migration and segregation amongst this goose population (MS2, MS6 and see **Chapter 6**). Geese breeding in the south of the breeding range tend to winter furthest north and *vice versa*. Hence, cooling in the north of the breeding range is likely to affect those geese that winter in Ireland and Wales more than those wintering in Scotland (MS2, MS27). Breeding success in the population is linked to June temperatures (Zöckler & Lysenko 2000). Some climate models predict that central west Greenland (between 67° and 69°N) will experience warmer springs which could improve conditions for geese breeding there (Rigor et al. 2000, W. Skinner *in litt.*). This is the area with the highest densities of summering Greenland White-fronted Geese, both breeding and moulting (MS23), and is thought to be the summering area of birds which winter predominantly in Scotland (MS2). It is also the area where breeding and moulting Canada Geese have increased greatly in recent years (MS13, MS22). During the moult, White-fronted and Canada Geese use the same habitats and areas adjacent to open water bodies to regrow flight feathers (see **chapter 7**). Canada Geese there breed in their third summer and produce more young per unit area than Whitefronts using the same habitats. Canada Geese are also behaviourally dominant over them there (Jarrett 1999, Kristiansen 2001). Since Canada Geese show no signs of reducing their rate of

expansion, they are likely to exert an ever greater influence on the endemic Greenland White-fronted Geese which used to be the only herbivorous waterbird in the region. Hence, inter-specific competition on the breeding areas could play a major role in the future population dynamics of Greenland White-fronted Geese. As many of the northern populations of geese continue to expand, use novel habitats and exploit new areas, the potential for competitive interactions increases. The need for an understanding of such processes in order to make predictions relating to the impacts of these interactions at the population level makes this particular study of broader ecological significance in the future.

What is clear is that the ecological conditions experienced by the geese will not remain constant and the benefits of existing information relating to population processes will offer some key to understanding how Greenland White-fronted Goose numbers will respond to change in the future. The future changes in distribution and abundance of this race of geese will not be any less interesting to follow than those in the past.

2.7 Conclusions and discussion

The traditional patchy bogland wintering habitat of the Greenland White-fronted Goose undoubtedly constrained population size in a landscape unchanged by Man's activities. Exploitation of this specific habitat is likely to have shaped highly site faithful behaviour and influenced the evolution of the prolonged parent-offspring relationships which distinguishes this population from most other goose species. Whilst habitat

destruction and hunting undoubtedly had a negative effect on population size, the recent colonisation of low-intensity agricultural systems and subsequent use of intensively-managed reseeded grasslands have permitted considerable extension to an otherwise highly conservative pattern of habitat use. Restrictions on winter hunting have resulted in an increase in numbers since 1982, such that it seems likely that there are now more Greenland White-fronted Geese than in the recent past, strongly suggesting that population limitation was previously related to factors operating on the wintering grounds. The provision of new improved grassland habitats during the 20th Century has permitted the colonisation of new, richer food sources by the population. Hunting in the period up to protection may have imposed population limitation on the wintering grounds prior to 1982. Hunting in Iceland is likely to continue to add to overall mortality in the population. The adequacy of site designation and conservation in Iceland needs to be considered in the context of the annual cycle. Extension of feeding to intensively managed agricultural grasslands available from the late 20th Century onwards has probably been responsible for the contemporary lack of population limitation through factors operating on the wintering grounds. Under protection, numbers have increased but show new signs of reduction in the rate of increase. New threats to the population from global climate change and competitive interactions with other herbivorous geese recently colonising their breeding areas underline the need for continued monitoring of the population. It is therefore important to initiate a specific study of the influence of climate on survival and reproduction amongst elements of the population in different parts of the breeding range.

3 Accumulation of body stores and the flight to Iceland

3.1 Introduction

Greenland White-fronted Geese return each year to Greenland for the summer. The challenge to each individual as daylength increases is to attain a body condition that will enable it to undertake spring migration, first to Iceland and thence over the Greenland Ice Cap to the breeding range on the west coast. To attain that body condition will, at minimum, involve the necessary mechanical adjustments to flight architecture and the accumulation of sufficient energy stores to sustain long distance migratory flight. How are these stores of protein and fat, respectively, accumulated through the winter and spring? When are such stores accumulated and what factors may affect the ability of an individual to reach the necessary minimum levels to start the flight northwards and to complete it safely? Most geese of the genus *Anser* reach sexual maturity at the age of 2 or 3 years (Owen 1980). Only a small proportion of Greenland White-fronted Geese more than two years of age breed successfully (see **chapter 6**). There may be different thresholds of stores accumulated *en route* to the breeding grounds that could affect the ability of an individual to reproduce successfully. For instance, stores of fat could be sufficient to provide a female with fuel for the entire journey and to invest in clutch initiation, but still fall short of the amount required to sustain the female through incubation. Under such circumstances, the relatively long-lived individual survives to attempt to breed in a subsequent year, despite failing to return with young in this particular season. Inability to accumulate fat stores sufficient to fly to Iceland in the first stage of migration would have a direct impact on the survival of the individual. The accumulation of body stores in anticipation of events in the annual cycle of the geese is therefore of considerable importance for the fitness of an individual and has consequences for the population, by having a direct effect on survival and reproduction.

3.2 Spring accumulation of body stores on the wintering grounds

Geese show a predictable rheostasis in body mass during the course of the winter. It is generally assumed that geese maintain a level of body stores

that represents a trade-off between the likely need to utilise such stores and the costs of maintenance. Most studies of waterbirds have shown a pattern of mass accumulation during autumn followed by a decline in winter and an increase in spring (e.g. Mallard *Anas platyrhynchos* Owen & Cook 1977, Dunlin *Calidris alpina* Pienkowski et al. 1979). However, relatively few studies have determined the change in body mass of geese at any one wintering area throughout the entire non-breeding period. In general terms, this represents a cycle of rebuilding depleted stores (generally of fat) exploited to fuel the often long flight from autumn staging areas. These fresh stores are hypothesised to be accumulated in anticipation of severe weather during the middle part of the winter. In mid-winter, limits to food intake, short foraging daylength and low temperatures may combine to necessitate the periodic use of such stores to supplement exogenous sources of energy (e.g. Ebbs 1989, Owen et al. 1992, but see also Therkildsen & Madsen 2000). In late winter, depletion of these stores often results in lowest levels of body mass as daylength increases, followed by a period of rapid accumulation of body mass in preparation for the spring migration towards the ultimate breeding areas (Owen et al. 1992), although such spring pre-migration fattening is not typical of all arctic-nesting geese (see Flickinger & Bolen 1979, Ankney 1982). Nevertheless, in several studied species, female geese may increase their body weight by 41-53% over winter levels (see for example McLandress & Raveling 1981).

Not all late winter/spring mass accumulation represents fat, since birds about to undertake a major migration episode after an essentially sedentary winter period are likely to have to reconstruct their (i) digestive and (ii) flight architecture (e.g. McLandress & Raveling 1981, Piersma 1990). These modifications enable more efficient accumulation of reserves and through shifting of internal protein reserves, the enlargement of breast musculature to sustain prolonged periods of flight (Piersma 1994). Whether mass changes in winter affect breeding success in geese has yet to be demonstrated, but there are clear links between breeding success and body condition in late spring (e.g. Ebbs 1989, Black et al. 1991, Madsen 1995). Hence, the mass dynamics of Green-

land White-fronted Geese in late winter and spring are at least likely to affect the ability of an individual to undertake the flight to Iceland successfully. Furthermore, the levels of stores available on departure from the wintering areas could potentially influence the extent of stores available for the onward flight to Greenland and ultimately for investment in reproduction. Clearly, any contribution that accumulated stores can make to body maintenance, egg laying and incubation (in the case of the female) and to territorial defence and mate protection (amongst males) is likely to contribute to the reproductive output of a goose pair.

In the case of the Greenland White-fronted Goose, there are three sources of proxy data that can be used to follow the changes in body constituents or in fat stores throughout the course of the winter. The first is the use of catch data from Wexford Slobs, where geese have been captured using cannon nets each year since 1983/84. All have been aged and sexed and weighed to the nearest 50 g before being fitted with individual marks and metal tarsus rings (see MS7 for full details). Most catching has taken place in the autumn, especially in October/November, but some birds have been caught in all months from October to April. Fitted regression lines to the full data set of indi-

vidual weight regressed on date shows a polynomial relationship between body mass and date for all age and sex classes (Figure 3.1). These patterns represent a slight decline in mass from arrival until December followed by a gradual accumulation until departure in early to mid April.

These data represent the cumulative data over many years, but the general trend from January onwards is confirmed by a second method. A series of catches carried out throughout the spring of 1999 specifically to assess within-winter patterns of body mass change concentrated on late winter/spring catches of small numbers of pairs. The results are shown in Figure 3.2 and confirm the general pattern of relatively slow accumulation of body mass throughout the latter half of the winter at Wexford.

The third proxy method of assessing body mass is the use of field scores of abdominal profiles of geese wintering at Wexford. Owen (1981) developed the use of abdominal profiles as a non-consumptive method of assessing the fat deposits of geese in the field. The method depends upon the fact that fat stored in the abdomen is a reliable index of general fat stores accumulated throughout the body (Thomas et al. 1983), and the levels of abdominal fat storage can be assessed using a

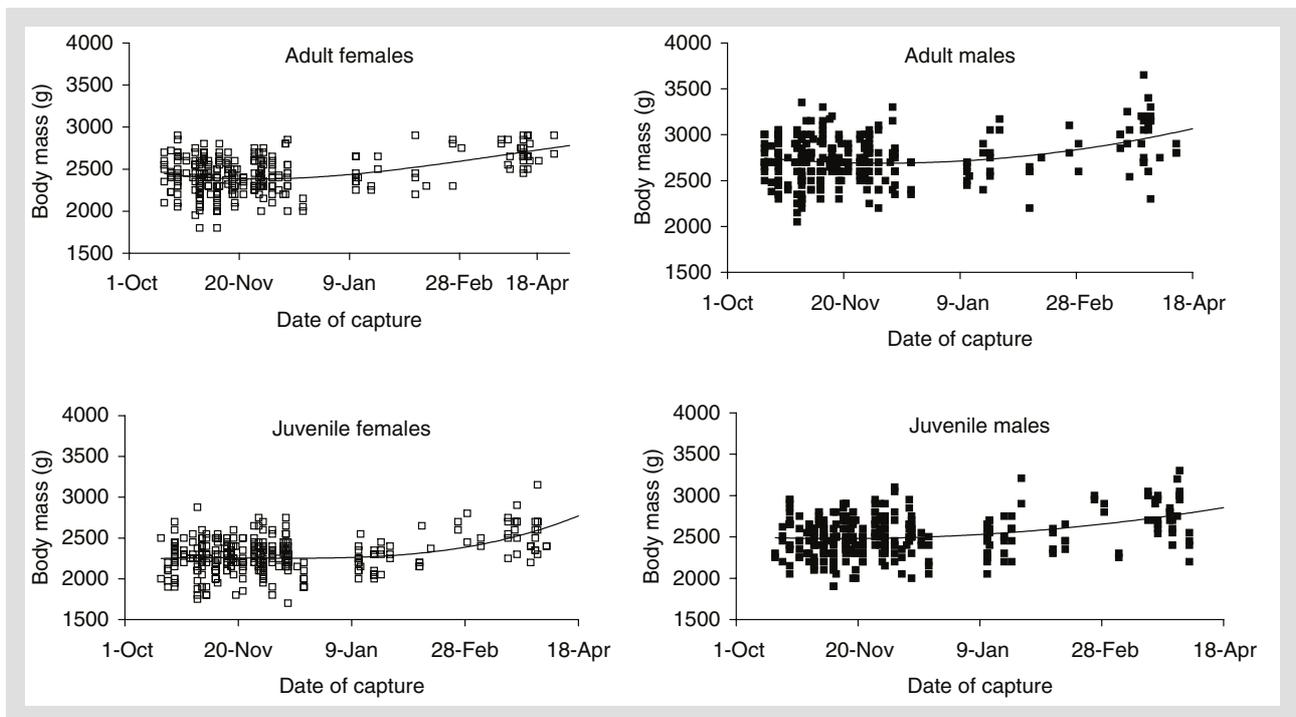


Figure 3.1. Body mass determinations of Greenland White-fronted Geese caught at Wexford during the winters 1983/84-1998/99 combined, showing fitted polynomial regressions (see Appendix 1 for statistics relating to figures¹).

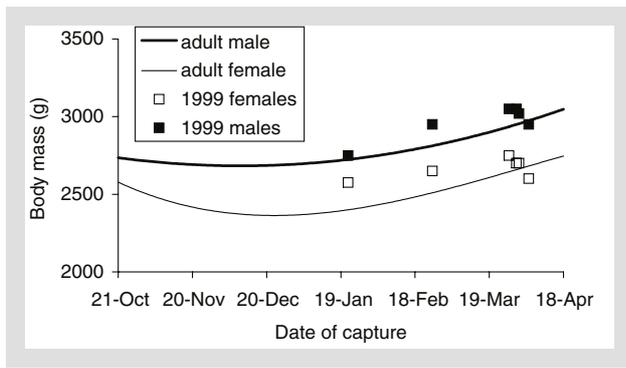


Figure 3.2. Body mass determinations of individual adult male and adult female Greenland White-fronted Geese caught at Wexford in spring 1999, compared to regression models for these age and sex classes from 1983/94-1998/99 combined (from Figure 3.1).

predetermined visual scoring system. In Greenland White-fronted Geese, there is a good correspondence between this measure and overall body mass (see **chapter 4**). This method of assessing changes in abdomen profile has been applied to collared individual Greenland White-fronted Geese wintering at Wexford Slobbs since 1984/85, enabling the compilation of median field scores for each half-month period there over many years. These values are presented in Figure 3.3, which demonstrates a remarkable degree of between year variation in arrival condition of birds in autumn, but a high degree of convergence towards attainment of similar scores by the time of the spring departure. Combining all years suggests little difference between the sexes in the rate of accumulation of abdominal fat stores (Figure 3.4). The patterns of change in this measure are very similar to those of direct body mass determina-

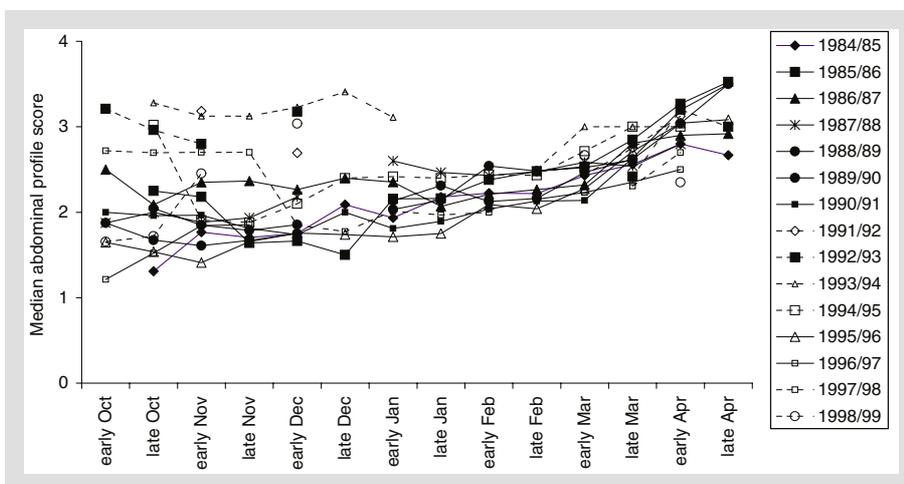


Figure 3.3. Half-monthly median abdominal profile scores of Greenland White-fronted Geese wintering at Wexford Slobbs, SE Ireland during the years 1984/95-1998/99.

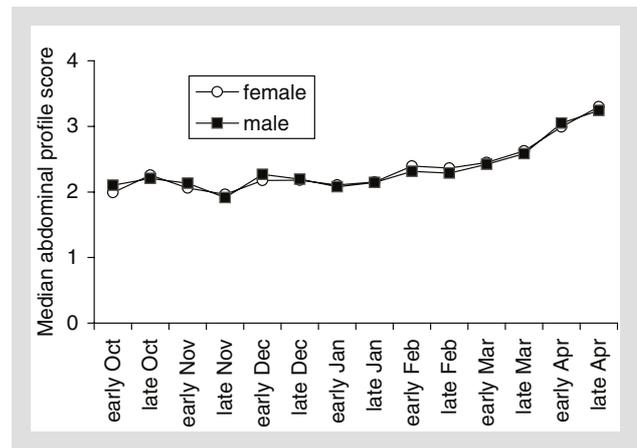


Figure 3.4. Half-monthly median abdominal profile scores for adult male and female Greenland White-fronted Geese wintering at Wexford Slobbs, SE Ireland for all years combined 1984/95-1998/99.

tion, suggesting that geese only gradually accumulate fat deposits over the period from mid December until their departure in mid April.

It would therefore seem that unlike other studied geese in winter (e.g. Svalbard Barnacle Geese wintering in western Scotland, Owen et al. 1992), Greenland White-fronted Geese at Wexford are generally able to maintain and even increase body mass during the short day lengths of December and January. This is probably due to the generally mild prevailing weather conditions and favourable feeding conditions at Wexford, which probably reflects conditions throughout much of the winter range. Mayes (1991) showed that only when ambient temperatures averaged -0.5°C in January 1985, and the frozen substrate precluded geese from probing for nutritious stolons, did Greenland White-fronted Geese lose condition at a semi-natural grassland site. Similarly, Stroud (unpubl. data) studying Greenland White-fronted Geese on Islay found median API scores fell by 1.4-2.0 units during the sub-zero temperatures of December 1980. Prolonged periods of frost and temperatures to -10°C at that time stopped grass production and denied geese access to peatland food items at the roosts.

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Because the winter range of the Greenland White-fronted Goose falls within the 3°C January isotherm (Belman 1981), the population rarely encounters periods of prolonged ground frost. Hence, although relatively low temperatures may stop or reduce grass growth, their propensity for grubbing and probing in soft substrates in semi-natural grass swards for stolons and nutrient rich overwintering plant parts (e.g. bulbils, rhizomes and other storage organs) enables the geese to maintain a nutrient and energy rich diet from December onwards. In addition, the mild oceanic conditions of their winter range reduces the costs of thermoregulation compared to, for instance, the Russian-breeding White-fronted Geese which winter in continental Europe (Mooij et al. 1999). Hence, the need of the Greenland White-fronted Geese to accumulate substantial stores necessary to balance the nutrient shortfalls in mid-winter (as a result of restricted food availability, feeding opportunity and/or enhanced energetic expenditure) may be less than in other waterbirds (e.g. Owen & Cook 1977, Pienkowski et al. 1979, Ankney 1982, Ebbinge 1989, Owen et al. 1992).

These data suggest that Greenland White-fronted Geese at Wexford do not rapidly accumulate stores in preparation for the spring migration to Iceland, as they have maintained condition throughout the autumn and early winter period, accumulating stores for migration over an extended four-month period. Nevertheless, birds do accumulate mass in late March and through April faster than at other times during the winter. This is still not as dramatic as in the Barnacle Geese that winter in southwest Scotland and migrate

first to stage in northern Norway before continuing northwards to their Svalbard breeding areas (Owen et al. 1992). Similarly, the Dark-bellied Brent Geese *Branta b. bernicla* show very much more rapid spring fattening immediately prior to migration from Western Europe to staging areas in the White Sea (Ebbinge 1989, Drent et al. 2000).

3.2 The costs of the flight to Iceland

Can we predict the amount of fat deposits a Greenland White-fronted Goose must accumulate in order to fuel the flight from the wintering grounds to the staging areas in Iceland? First, we have to understand something about the nature of the migration flights between wintering areas and spring staging sites: how far do geese fly, how fast and how often do they rest? In 1997, a project was started to affix satellite transmitters to Greenland White-fronted Geese on the wintering areas in Ireland in order to track the migratory behaviour of known individuals *en route* to their summering areas (MS20). The regular signal produced by the radio transmitter is detected by orbiting satellites above that enable the precise position of the transmitter to be determined at given intervals. In this way, it is possible to track the migration routes, duration and speed of individual Greenland White-fronted Geese moving from Ireland to Iceland and subsequently from Iceland to their ultimate breeding areas in west Greenland. These studies showed that the geese flew directly from Ireland to staging areas in Iceland in three different springs along a narrow migration corridor. All maintained ground speeds of 50-90 km

Table 1.1 Estimated fat requirements (in g.) for the flight in still air of a male and female Greenland White-fronted Goose from Wexford, Ireland to Hvanneyri, western Iceland on spring migration, based on four different formulae (see text for further details).

	Flight speed (km/hr)	McNeil & Cadieux (1972)	Summers & Waltner (1978)	Greenewalt (1975)	Davidson (1984)
Male lean mass 2.6 kg	50	268	252	292	254
	60	221	208	292	211
	70	188	178	292	180
	80	164	155	292	157
	90	145	138	292	139
Female lean mass 2.3 kg	50	246	237	272	240
	60	202	196	272	199
	70	172	167	272	170
	80	150	146	272	148
	90	132	130	272	131

h^{-1} and none showed any sign of resting on the sea *en route*.

A number of different approaches have been made to estimate the energetic costs of flights for birds of different sizes. The simplest approaches have been those methods, which use crude estimations of the energetic costs of flight. Based on simple energetic formulae, it is possible to estimate the costs of flight to Iceland from Wexford. Given that many Wexford wintering birds stage at Hvanneyri in western Iceland (MS27), the distance between these two areas (1,500 km) was used to calculate the minimum flight range necessary for geese to reach their staging site. The still-air flight-range estimation methods of McNeil & Cadieux (1972), Summers & Waltner (1978), Greenwalt (1975) and Davidson (1984) were used to back-calculate the minimum fat stores necessary to sustain flight over that distance. These were used to generate a range of different speeds for a female of departing lean body mass 2.3 kg and a male of 2.6 kg (see Table 3.1). Given the observed ground speeds of 50-90 km h^{-1} observed amongst satellite tagged geese making this journey, a range of values were obtained for these observed speeds. These suggest that males require between 145 and 292 g of fat and females 130-272 g fat to fuel the passage from Wexford to Hvanneyri.

A more sophisticated method is to attempt to model the birds rate of use of fuel, based on the mechanical work the organism must do, given its morphology and the conditions of flight. This is the aerodynamic approach of Pennycuick (1989), which makes several assumptions about the physiology of flight, but nevertheless provides the best predictive model available at the present. The most recent version of his software (Flight.bas version 1999) was used which incorporates findings from recent wind tunnel studies which suggest that even for a large birds like a goose, the coefficient of body drag (C_{db}) is lower than previously thought (Pennycuick et al. 1996). In the present analysis, the suggested lower value ($C_{db} = 0.10$) was used instead of 0.25 (see also Green & Alerstam 2000). The results are shown in Figure 3.5, showing the range of flight range estimates for a female of lean body mass 2.3 kg and male of lean body mass 2.6 kg, the 1500 km flight necessitating 340g and 349g of fat for the male and female respectively. Both calculations make the assumption that the geese fly at maximum range speed, which was 99 and 103 km/hr respectively.

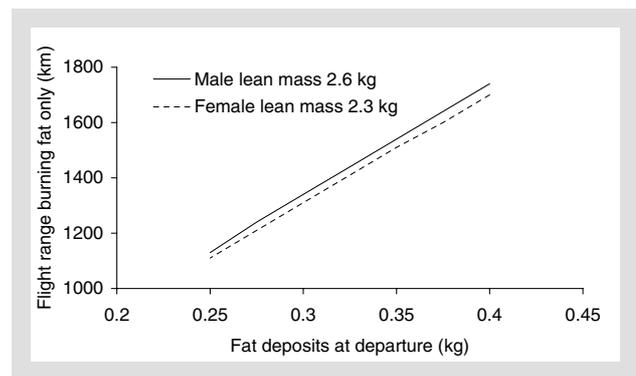


Figure 3.5. Theoretical flight range estimates for male and female Greenland White-fronted Geese of lean body mass 2.6 and 2.3 kg respectively, given different fat loads at point of departure based on Pennycuick models (see text for details).

At lower speeds, for the same total energy expenditure, the flight range estimate would be reduced (Figure 3.6).

Despite considerable monitoring efforts, it is clear that we still know very little about the prelude to departure of the geese from their wintering grounds in spring. All of the data presented above derive from the main Irish wintering site, and nothing is known from wintering sites elsewhere. Satellite telemetry (MS20) showed that in a spring when a relatively early departure occurred from Wexford, at least one of the early departing birds fitted with a transmitter left Wexford on 10 April 1997, but staged on the northern Ireland coast until 16 April before departing for Iceland. Such spring staging within Ireland may be simply due to birds responding to initial cues, which suggested that weather conditions were favourable for migration, only to encounter unfavourable conditions later on. Resightings of Wexford-wintering birds seen soon after spring departure on

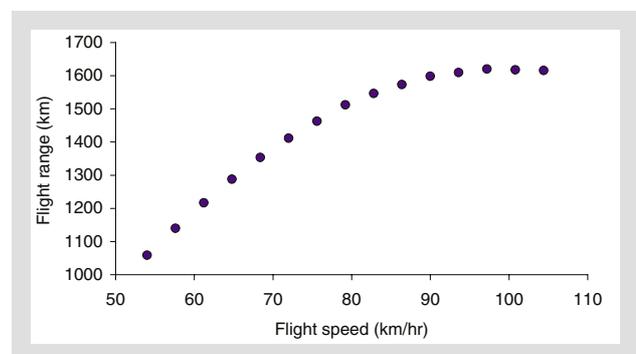


Figure 3.6. Effects of differences in flight speed on the theoretical flight range of Greenland White-fronted Geese.

the Outer Hebrides and Islay in Scotland suggests geese have the option to stop off at more northerly staging areas within Britain and Ireland after departure from further south (for whatever reason). Certainly there was evidence in 1997, 1998 and 1999 that geese departed from Wexford shortly after the wind had swung to a southerly direction (MS20). Geese are likely to save considerable energy by using a following assisting wind compared to making the flight with head- or crosswinds. A full analysis of prevailing meteorological conditions associated with migration episodes is currently underway, as is a full analysis of the energetic costs of the migration from Wexford to staging sites in Iceland.

3.3 The mass gains in Ireland during winter

From the catch data, it is possible to estimate from the fitted regression models the difference in body mass between the lowest mean weight (the point of minimum inflection derived by differentiation for the model) and the mean weight around normal departure time (taken to be April 20). The difference is $3077-2690 = 387$ g for males (14% increase) and $2787-2380 = 407$ g for females (17% increase). It is unlikely that mid-winter weights represent fat-free mass. Stroud (unpubl. data) found significant deposits of mesenteric fat in dissections of Greenland White-fronted Geese shot on Islay throughout the winter. Between 9 and 48 g of fat of this form (0.3-1.9% body mass) were recovered from individuals throughout January (D.A. Stroud in litt.), although measures of other fat deposits were not available from these birds.

McLandress & Raveling (1981) found that 61% of weight gain between mid winter and spring migration departure in male Giant Canada Geese *Branta canadensis maxima* was lipid and 47% in females. Corresponding proportions of fat in weight gains for migrating waders vary between 50 and 100% (see Zwarts et al. 1990), with measured values of between 60% (McNeil 1969, 1970) and 90% (Summers et al. 1987, 1989). However, it is unlikely that all of the difference in mass accounted for is fat, indeed larger birds (such as geese) tend to incorporate a greater proportion of non-fat components when increasing body mass (Lindström & Piersma 1993). In the Greenland White-fronted Goose, 60-90% of the weight increase representing fat would represent an accumulation of 232-348 g fat in males and 244-366

g in females. Mid-winter weights of White-fronted Geese in North America include 12-16% fat content, which would equate to an additional 286-381g of fat in females and 323-430g in males. Although these calculations make a number of important assumptions, on this basis, the total average fat content of Greenland White-fronted Geese on departure could constitute sufficient energy source to sustain the flight to Iceland using fat only as a source of energy. Based on these average values, geese also have the potential to supply the energy needs from stores for self-maintenance in Iceland for several days after arrival, should they encounter restricted feeding opportunities.

3.4 Conclusions & discussion

Greenland White-fronted Geese show variable levels of body mass throughout the season, but unlike the few other studied populations, at Wexford they maintain, or only slightly lose mass through mid-winter. After mid December, mass is accumulated increasingly until departure in mid-April. On the basis of various theoretical approaches, geese need to amass fat stores of 150-340 g (females) and 139-349 g (males) to fuel the flight to staging areas in Iceland. If it is assumed that (i) mid-winter minimum body mass represents lean body mass (unlikely based on other body composition studies of *A. albifrons*) and (ii) that 80-90% of the increase to departure weight represents fats store accumulation, based on average body mass determinations, then Greenland White-fronted Geese attain sufficient fuel for the spring flight to Iceland. If the minimum mid-winter mass includes fat reserves, geese retain substantially more fuel than required for the journey to Iceland. However, the distance involved means that the geese could not fly direct to Greenland from the wintering grounds, a distance of more than 2600 km.

More detailed analysis of the satellite telemetry data, incorporating real-time meteorological conditions prevailing at the time of the migration episodes, is required to determine the precise energy requirements of the geese during these specific migration flights. It would be highly instructive to use heart beat as an alternative method to independently measure fuel consumption during migratory flights (as used by Butler et al. 1998). Until full analysis of the fat dynamics of White-fronts is carried out (e.g. using non-destructive techniques such as the use of doubly

labelled water), the precise extent, duration and rate of fat store deposition on the wintering grounds prior to migration cannot be accurately determined. Similarly, there is a need to determine changes in organ size associated with this period of body mass gain to determine what other changes in body state occur during the prelude to migration. Since it is to be expected that a number of external factors affect the rate at which individuals accumulate these fat and other stores (e.g. human disturbance, access to feeding oppor-

tunity as a result of social status, differences in habitat quality and predation risk) it would be highly instructive to co-ordinate such studies on individuals in differing wintering situations. Because of great variation in habitat quality on the wintering grounds and the apparent difference in trends in numbers at the different resorts, it is important to establish the role these factors play in determining survival, emigration and fecundity rates amongst these different elements of the population.

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4 Spring staging in Iceland and the flight to Greenland

4.1 Introduction

Until the 1980s, little was known about the status of staging Greenland White-fronted Geese in Iceland. It was known that large numbers passed through Iceland in autumn, but now it is known that the population also stops there in spring *en route* to the breeding grounds (MS4). It is clearly important to establish whether, where and for how long birds stage on spring migration since feeding at staging sites enables individuals to recoup depleted energy and nutrient stores and hence potentially affect subsequent breeding success (see review by Thomas 1983). Weather conditions in Iceland in spring had been shown to correlate with subsequent breeding success of the Pink-footed Geese *Anser brachyrhynchus* which nest there (Fox et al. 1989). Hence, it was reasonable to assume that weather conditions and the availability of forage were likely to affect the condition of migrating Greenland White-fronted Geese departing for the breeding grounds from Iceland in spring. During the late 1980s and throughout the 1990s, a series of studies were carried out examining the spring staging of different goose species in Iceland, to assess the importance of feeding ecology of pre-nesting staging in that country. An important aim was to establish the importance of specific staging areas and to assess the distribution and abundance of the different goose populations there, examining the use of different habitats and the way in which the geese exploit these (e.g. Boyd & Fox 1992, 1995, Fox et al. 1991, 1992, 1994a, 1994b, 1999). In very recent years, these studies have involved a Ph.D study (Kristiansen 2001) and Masters student study (Nyegaard 2001), but from which selected results are presented here.

In conservation terms, the most important elements in the study of spring staging relate to the identification of staging areas, the habitats and food plants used by the geese, the level of energetic gain that can be achieved by geese utilising different habitat types and how they may derive the maximum nutritional benefit from them. In this way, it is possible to establish some basis for ranking the importance of sites and habitats in terms of the number of birds using different sites for site safeguard and nature conservation management purposes. Finally, studies have also con-

sidered how much nutrient gain can be derived from the staging period in Iceland during the prelude to migration over the Greenland Ice Cap to the breeding grounds on the west coast.

4.2 Distribution of spring staging Greenland White-fronted Geese in Iceland

Observations from many years confirm that a large proportion (if not all) Greenland White-fronted Geese stage in Iceland from c. 10 April to c. 12 May in most seasons (MS4, MS19). At this time, they use two main areas, namely the southern lowlands (Árnessýsla, Rangárvallassýsla and Vestur-Skaftafellssýsla) and the western lowlands (Kjósarsýsla, Borgarfjarðarsýsla, Mýrarsýsla and Snæfellsness- og Hnappadalssýsla). Spring migration phenology appears to differ between areas, with earlier arrivals but a slower build-up to maximum numbers in the southern lowlands. Here, numbers peaked during 24-26 April in 1990-1992, but dispersed earlier compared to the rapid build up in western staging areas to peak numbers during 18-22 April in 1997-1999, where substantial numbers of birds remained well into May each year (MS19). These differences most likely relate to the timing of migration in the years concerned, but could also reflect different migration strategies of birds using the two areas (records of individuals using both staging areas are rare, MS27). The southern lowlands, especially along the coast, experience a slightly milder climate and hence earlier thaw than the west, which may initiate plant growth a little earlier in the spring. In addition, there are substantial areas of tillage in the southern lowlands that do not occur in the west (see below).

At the most important staging site in the western lowlands, Hvanneyri, up to a maximum of 1,600 birds have been counted (MS19). Based on observations of individually marked birds at Hvanneyri, more than half of the geese remained for less than a week, mostly early on in migration, whilst more than a third stayed for almost the entire staging period (c. 24 days).

From observations of individually marked Greenland White-fronted Geese, at least 90% of goslings

associate with their parents and siblings in Iceland in their first spring. All reported subsequently have been seen within 4 km of where they were seen in their first spring with their parents (MS27). As on the wintering grounds (MS7, MS9), individuals show a high degree of within- and between-season site fidelity in Iceland. Some 96% of multiple within-spring resightings of individuals were within 4 km of each other, although 3 geese moved 88 km from the southern to the western staging areas. Four percent of geese seen in two consecutive springs and none seen in consecutive autumns moved more than 4 km between years. By contrast, significantly more (12%) moved more than 4 km in subsequent seasons between spring/autumn and autumn/spring. All these shifted within the western lowlands to or from Hvanneyri in autumn, the only declared hunting-free area for Greenland White-fronted Geese which are otherwise legal quarry throughout Iceland in autumn. Scottish-wintering birds were more likely to use southern staging areas and generally Wexford (Ireland) wintering birds were more likely to stage in the western lowlands of Iceland in both spring and autumn (MS27). Since Scottish wintering birds tend to breed in the south and central part of the breeding range, and Wexford-wintering geese generally summer in the north of the range, there may be some basis for genetic isolation amongst different elements of the population (MS2, MS6). The methods used in this investigation are likely to overestimate levels of between season site fidelity, so these results should be interpreted with caution. The use of other independent methods (such as the use of data from satellite tagged individuals) is necessary to validate current estimates.

4.3 The costs of the flight to Greenland

Based on the results of the satellite telemetry project, Greenland White-fronted Geese flew another 1,500 km from the west Iceland staging areas to their arrival points in west Greenland (MS20). The energy requirements necessary to complete the flight would be the same as the Ireland-Iceland flight, if the geese did not have to cross the Greenland Ice Cap. In the early 1980s, it was unknown whether geese did traverse the Ice Cap, or rather migrated along the west coast to and from the southern most point. Since that time, it has been shown that such a long journey around Kap Farvel to avoid climbing to cross the interior ice offers no increased efficiency to migrating

geese (Gudmundsson et al. 1995). Radar observations and investigations have shown that geese cross the Ice Cap in both spring and autumn (K. Vægter, pers. comm., Alerstam et al. 1986). The satellite tagged individuals took this route in spring, passing over the Greenland Ice Cap where this reaches to *c.* 2,800 m above sea level (MS20). Therefore, geese would also have to expend the energy required to climb to this altitude. Given a female goose starting this climb with a body mass of 2.3-2.9 kg and a male of 2.6-3.3 kg, the force required to lift these masses to 2800 m would be $6.3-8.0 \times 10^4$ Newtons for females, and $7.1-9.1 \times 10^4$ for males. If it is assumed that there is an energy conversion efficiency of 0.23 and that aerobic bird flight is fuelled by fat (with an energy density of $3.9 \times 10^4 \text{ J g}^{-1}$, Pennycuick 1989), this is equivalent to an additional 70-89 g of fat for females and 80-101 g of fat for males to accomplish the additional physical work required to fly up and over the Ice Cap. On this basis, the fuel requirement to make the second leg of the spring journey would be between 200 and 429 g for females and 219-450 g for males.

The accumulation of stores in Ireland in preparation for the flight to Iceland is dispersed over almost 4 months. At similar rates of accumulation, the mean stopover time in Iceland does not permit the geese to achieve similar rates of gain during the average of 18 days the satellite tagged geese remained there in spring (MS20). We need to know how fast geese can potentially accumulate stores in Iceland, and in order to do so, we need to understand something about their body condition immediately after arrival in Iceland, track the rate of change and assess their departing condition at the time they set off for West Greenland. Furthermore, we need to be able to assess whether different feeding strategies adopted by the geese enable some individuals to better accumulate stores than do others.

4.4 Mass gains in Iceland in spring

We have two independent means of assessing the spring accumulation of body mass during the stopover of Greenland White-fronted Geese in Iceland. Geese were captured at Hvanneyri in 1999 throughout the spring staging period. The change in body mass of adult males and females with time are shown in Figure 4.1. The best fit regression model was a simple linear form. Based on these models and an average arrival date of

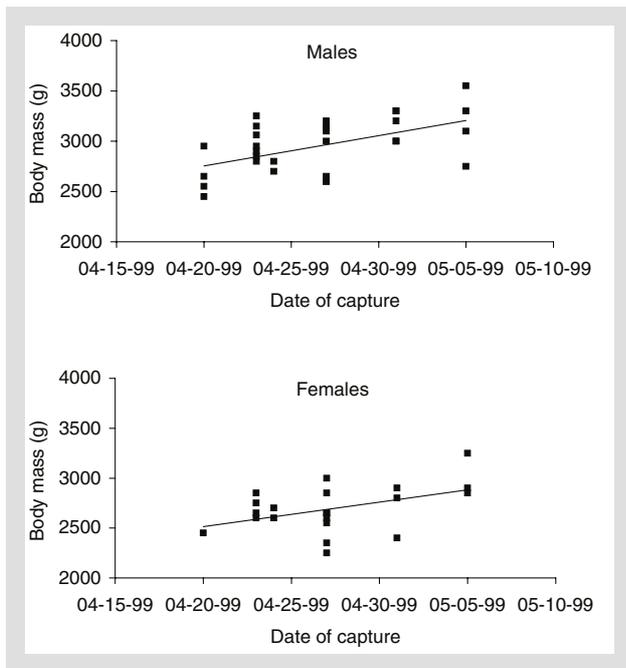


Figure 4.1. Changes in body mass of staging adult male and female Greenland White-fronted Geese caught at Hvanneyri, west Iceland in spring 1999. Fitted regression lines are best fit least squares linear regression models.²

20th April 1999 (MS19), the average body masses of arriving birds were 2.75 kg (adult males) and 2.51 kg (adult females). Assuming that the birds arriving at Hvanneyri were a representative sample of those departing Wexford, this meant that in 1999, geese arriving in Iceland had used 327 g and 277 g of fat respectively, assuming all the difference to be fat. This is slightly less than predicted by the Pennycuick calculation, but more than by the energetic flight range methods. However, these calculations are based on average values, and may not represent the true situation during the 1999 spring migration episode. These estimates suggest that the geese had not depleted all the reserves accumulated over the mid-winter minimum body mass in Ireland (see **chapter 3**). Using the same regression models, and a mean departure date of 5th May 1999 (MS19), geese accumulated an average of 369 g (15% in adult females) and 451 g (a 16% increase in body mass in adult males) during their 15-day stay in Iceland. These data are based upon observed lengths of stay of collared birds at Hvanneyri, which were slightly shorter than the average for the satellite tagged individuals. Nevertheless, the accumulation of 24.6 and 30 g body weight per day for females and males respectively is impressive during this short stopover. Their estimated mean departure masses were thus 3.21 and 2.88 kg (for

adult males and females) when departing for west Greenland from Hvanneyri, 129 and 96 g respectively heavier than the departure mass from Ireland.

An alternative approach is to establish a calibration factor for field scores of abdominal profiles, based on the body mass of known individuals of known abdominal profile scores. There was a good correlation between the API score and body mass amongst the geese caught at Hvanneyri (Figure 4.2). Since large numbers of geese were scored every day at Hvanneyri (although not specifically assigned to sex class), this enables the generation of mean body mass values for geese staging at the farm using the relationships shown in Figure 4.2 and assuming a sex ratio of parity. The results of this are shown in Figure 4.3. Mass accumulation does not appear linear (as suggested by catch data alone), suggesting that the catch data may actually slightly underestimate mass accumulation by the end of the staging period. Because the caught birds were cannon-netted over bait, it could be that the capture technique selected for birds in poor condition attracted to rich sources of food.

Despite the many assumptions made in these simple calculations, it does appear that geese arrived in Iceland with a residue of the body stores accumulated on the winter grounds and then very rapidly increased body mass there. If it is assumed that the geese at Wexford are typical of those else-

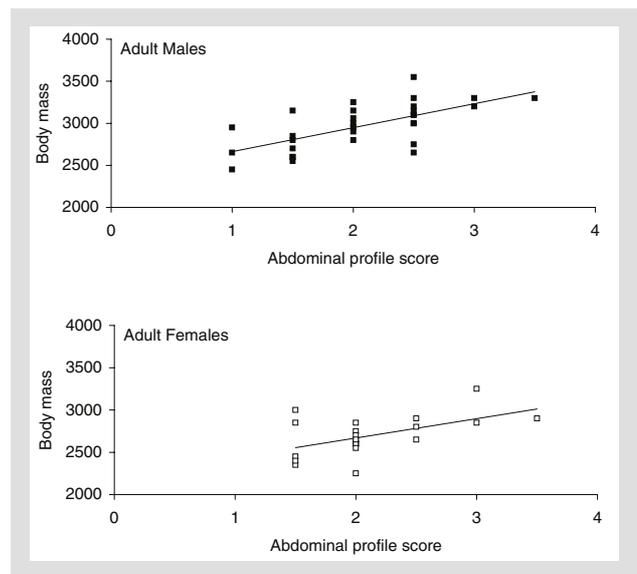


Figure 4.2. Relationship between abdominal profile score and body mass of captured adult male and female Greenland White-fronted Geese at Hvanneyri, spring 1999.³

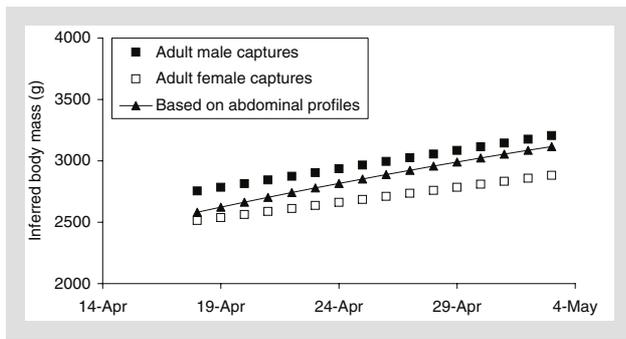


Figure 4.3. Comparison of change in daily median abdominal profile scores of Greenland White-fronted Geese recorded in the field and back converted to body mass from the calibration curves shown in Figure 4.2, compared with fitted regression models for change in body mass obtained from catches (shown in Figure 4.1).

where in the wintering range and that all geese accumulate mass at the same rate as those captured, the geese departing Hvanneyri left with 516 g (adult males) and 503 g (adult females) more body mass than the mid-winter minimum mass level. Assuming this increase includes 60-90% fat, departure fat stores would amount to 302-453 g (females) and 310-464 g (males). Again, this certainly underestimates the true extent of fat deposits, since mid-winter mass is unlikely to represent lean mass levels. Abdominal profile measures suggest this may underestimate slightly the true rate of increase amongst the geese at Hvanneyri. Given that a substantial proportion of this accumulation in Iceland was required to restore fat depots and that the mid-winter minimum mass included some fat reserves at that time, this is a substantial and adequate source of fat to fuel the crossing of the Denmark Strait and ice cap to the summering areas beyond.

4.5 Habitat utilisation in Iceland in spring

Greenland White-fronted Geese probably traditionally used as their natural food source the lower stem storage organs of *Eriophorum angustifolium* and *Carex lyngbyei* that grew in abundance in the lowland wetlands as their natural food source (MS4, MS19, MS27). Although the area of intact mire and undamaged wetland in southern and western Iceland remains large, despite much drainage in the 1970s and 1980s, it is clear that most spring staging Greenland White-fronted Geese now exploit agricultural grasslands. The most favoured grasslands are short-cropped hay-

fields that offer the most open dense swards, which exhibit rapid growth in spring. The geese glean waste from the harvests of previous autumns in the form of potatoes (especially in the Þykkvibær area of Holt) and barley (especially in the Hvolsvöllur area in Hvolhreppur) in the southern lowlands, as these are released from the winter snow prior to ploughing. Such crops are not cultivated to any great extent in the west (MS24).

The results of detailed studies at Hvanneyri have shown that spring staging geese differentiate between different grassland sward types on the basis of food quantity and quality (MS15, MS16, MS24, MS25, MS26, Nyegaard 2001). The geese feed on all three of the most abundant grass species occurring in the sward, namely *Phleum pratense*, *Poa pratensis* and *Deschampsia caespitosa*, but each species is exploited in different ways and at different times according to growth form. *Alopecurus pratensis* also occurs, but is not especially favoured by the geese.

The fields at Hvanneyri can be classified as being dominated by one or other species of grass (where one species constitutes more than 50% of the sward) or are co-dominant (i.e. where 2 species of grass differ by less than 20% in their coverage). Combining cumulative goose counts from all classified fields at Hvanneyri shows that *Phleum* supports significantly greater densities of geese than *Poa*, *Deschampsia* or *Alopecurus* dominated fields (see Figure 4.4), although the last species was only present in very mixed swards on 5 of the fields. A

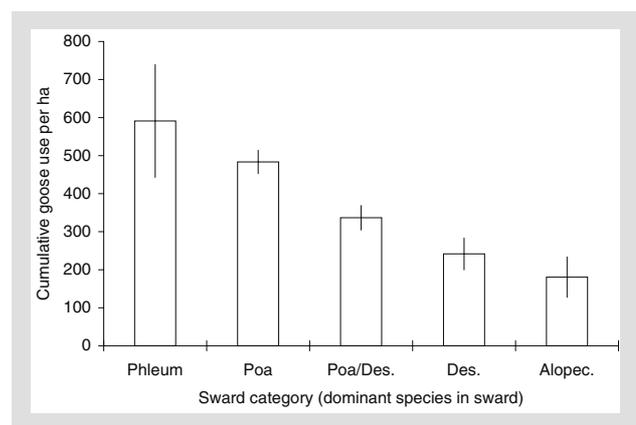


Figure 4.4. Cumulative goose use of fields of different sward composition, expressed as total geese per hectare (+ SE) during the spring staging period at Hvanneyri in 1997. Swards were composed of dominant *Phleum pratense*, *Poa pratensis*, *Deschampsia caespitosa* and *Alopecurus pratensis* or co-dominant *Poa/Deschampsia* as indicated.

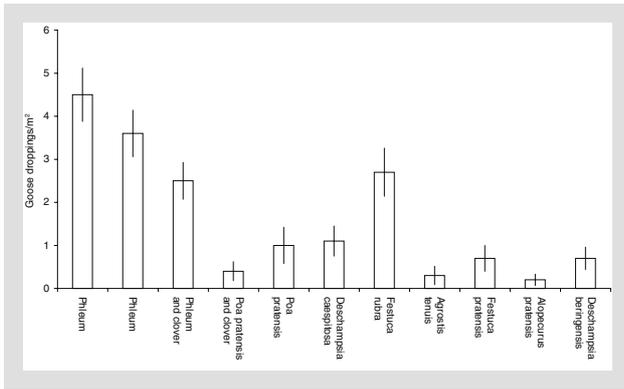


Figure 4.5. Dropping density (as an index of goose use + SE) of pure sown stands of different grass species in seed trial plots in a single field at Hvanneyri from spring 1997.

similar pattern can be seen based upon mean dropping densities (as an alternative assessment of goose use) in plots of sown single species stands of different grass species on trial plots within one field at Hvanneyri in 1997 (Figure 4.5). Note that the young establishing *Deschampsia caespitosa* formed a continuous open sward prior to tussock development and for this reason was therefore probably as attractive to geese as *Poa*.

The total goose use of any particular field can be seen as the product of 4 elements over time:

- 1) food density (which in turn determines the settlement density of geese)
- 2) food intake rate (which determines food depletion rate)
- 3) the 'giving up' density of food (the threshold at which the food resource is depleted to the point where it is more profitable to forage elsewhere)
- 4) the rate of regrowth of forage plants (which determines the time until the food resource exceeds the 'giving up' density of food and geese return for sequential harvesting)

In the context of individual field units, containing grasslands of different sward composition, the settlement density represents the aggregative response of geese as predators to their 'prey' (i.e. grass blades, MS26). The length of stay of geese in that field represents the interaction between standing crop biomass and intake rates (i.e. the rate of depletion of prey items down to a threshold 'giving-up' density). Finally, the length of absence is defined by the regrowth rate and quality of the prey to the point where this exceeds a profitability threshold for the geese, at which time

they will return in appropriate numbers to regraz the accumulated green biomass regrown in their absence.

The three major grass species differ in their quality, biomass accumulation and growth pattern. The *Phleum* is an ecotype introduced from Norway, valued for its early season growth, which commences before other grasses begin above ground production. Even in the early stages of growth, this species responds to defoliation by geese by increasing leaf elongation and elevated protein levels, a feature which together with its growth form, makes it the most attractive forage species for sequential harvesting by geese (MS15, MS25, MS26). After reseeding of a field with *Phleum*, leaf densities are high, but as the tussock-forming *Deschampsia* and the stoloniferous *Poa* invade, densities of *Phleum* decline rapidly (Fox 1993). In the early stages of the spring staging period, geese therefore assort themselves in response to the shoot densities of this, the most abundant green plant material available (MS26), although geese select for the longest leaves (MS25). As a consequence, highest densities of geese tend to settle on *Phleum* fields and eat out most leaves of suitable length, returning only when regrowth has occurred above a threshold bite size (Figure 4.6, MS15).

Poa grows at very low leaf densities and although of moderate nutrient quality, its later and (in some years) faster growth rate results in supporting lower densities of grazing geese throughout the staging period (unpublished data). In contrast to *Phleum*, where the high quality (low fibre, high protein) youngest leaf is always removed, leav-

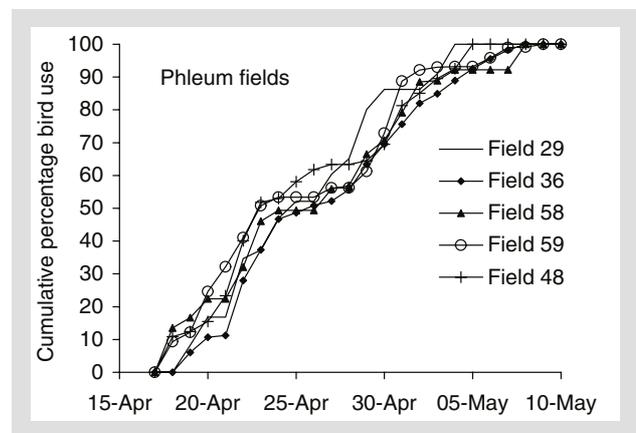


Figure 4.6. Cumulative goose use of five hayfields dominated by *Phleum pratense* at Hvanneyri in spring 1997. Note the rapid exploitation episodes, followed by short periods with reduced or little exploitation.

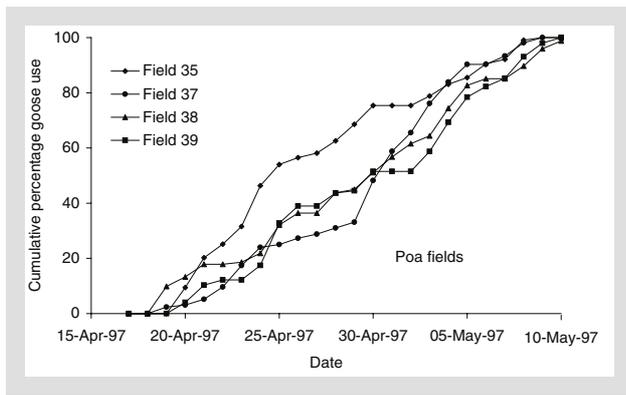


Figure 4.7. Cumulative goose use of four hayfields dominated by *Poa pratensis* at Hvanneyri in spring 1997. Note the lack rapid of exploitation episodes but more constant exploitation throughout the staging period.

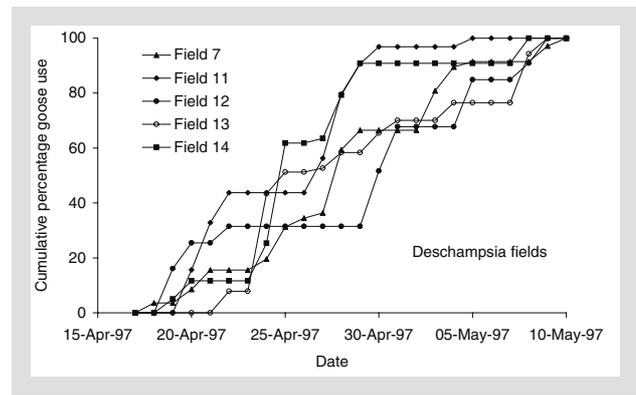


Figure 4.8. Cumulative goose use of five hayfields dominated by *Deschampsia caespitosa* at Hvanneyri in spring 1997. Note the very short intense exploitation episodes, followed by long periods of little or no exploitation.

ing the photosynthetically active older leaves intact, defoliation of *Poa* invariably removes the longest green leaf, with subsequent regrowth of the youngest blade (Therkildsen & Madsen 1999). Regrowth is generally moderate, but the low density of plants results in low goose densities which are maintained throughout the staging period, with little sign of sequential harvesting evident in the other species (Figure 4.7).

Deschampsia has a slow and asymmetric growth form, developing highest densities of fastest growing leaves on the south-facing sides of tussocks (MS16). Although the leaves have high protein content, they are slow to develop, and the patchy nature of the tussock form and the high levels of litter associated with *Deschampsia*-dominated fields results in low biomass and slow regrowth rates after defoliation. After such a field has been exploited, there is a long delay before geese return to graze the slowly accumulating regrowth (Figure 4.8).

Not only are the grass sward types utilised differently and hence support different goose densities, but individual geese show differences in their use of sward types (Figure 4.9). Birds such as 0CY and 2MY specialised on *Poa* fields and were consistent between years, 3KJ spent most time foraging on *Phleum* dominated fields, despite their overall rarity (there being only 5 or 6 such fields out of 62 in all three years of the study). H4A mainly exploited *Deschampsia* fields. Only D9X, a gosling hatched in 1996, associating with its one surviving parent and two siblings in all 3 springs, showed any great sign of change in sward selection. In 1997, it was associated with the six

Alopecurus fields, but used *Phleum* increasingly in the following years.

It is far from clear whether these patterns of use are more the result of the restricted home ranges of the individuals concerned than habitat selection *per se*. In all three years of observation, 0CY and 2MY were confined to the same 11 and 12 fields respectively and 3KJ was only ever reported from 5 adjacent fields in 1997 and 1998. By contrast, D9X and associated family members were recorded using 23 different field units in the three springs they were observed, with no overlap in home range between 1997 and the following two springs (when their use of fields was restricted to 11 fields with a higher degree of overlap). Wheth-

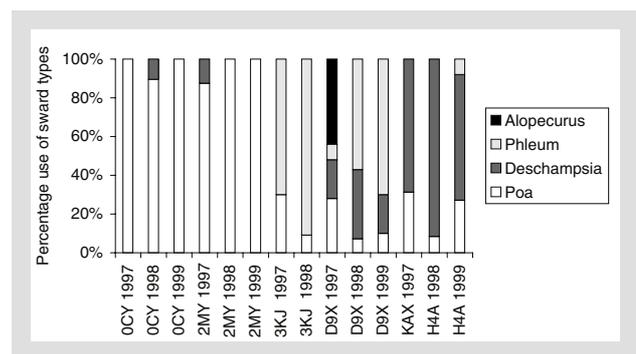


Figure 4.9. Use of different hayfield sward types by individually collared Greenland White-fronted Geese staging at Hvanneyri in more than one spring during 1997-1999 inclusive. Birds are identified by the 3 letter/digit collar code and the years of observations. Note the consistency of sward use by 0CY, 2MY, 3KJ and H4A in the years of observation that reflect consistency of field use as well as sward type. D9X (a juvenile with its parents in 1997) increasingly used *Phleum* dominated fields over the period.

er 3KJ was a behaviourally dominant individual able to win agonistic encounters in order to retain access to the *Phleum* fields, or whether the rare forays of H4A into *Phleum* swards were simply lack of experience or knowledge is impossible to determine. Aggressive encounters between geese were very rarely observed away from sources of water, so it seems unlikely that overt interference determines access to highest density or highest quality food (MS26). Nevertheless, there is no doubt that the use of different swards in different fields has some effect on the rate of accumulation of body stores for the next migration episode onwards to west Greenland (MS18, Nyegaard et al. 2001). Hence, it would appear that this presents a potential mechanism by which different individuals, staging on the same farm, exploiting different fields, may depart from Iceland having accumulated different levels of body stores because of their access to different hayfields during their period of spring staging.

We still know very little about the extent and importance of feeding on natural wetlands in Iceland. Certainly the rhizomes of *Carex lyngbyei* have a very high metabolizable energy content in spring (McKelvey 1985) and it is important in the nutritional ecology of other northern waterfowl (Grant et al. 1994). Significant numbers of Greenland White-fronted Geese feed on *Carex* meadows, especially in the middle part of the staging period in the Borgarfjörður region where such habitat is extensive. This suggests that this habitat could be an important supplement to grassland feeding, either for the population as a whole, or perhaps for individual birds that specialise on this food. The same is true for the *Eriophorum angustifolium*-dominated wetlands, where it is known that some birds exploit this food in the absence of alternative grasslands (because such hayfields do not exist in the vicinity). At Hvanneyri at least, based on observations of colour-marked individuals, it is known that geese that specialise on hayfield feeding do take to *Carex lyngbyei* meadows and *E. angustifolium* wetlands at certain periods during spring staging. Whether this is due to depletion of the grassland resource or improvement in the quality and/or availability of these natural foods is a subject of continuing investigation.

4.6 Conclusions & discussion

Greenland White-fronted Geese arriving in Ice-

land after the 1999 spring migration from Ireland were on average 277 g (females) and 327 g (males) lighter than mean departure mass in Ireland. Assuming these mean values represent the real costs of flight over the distance involved, this is less than predicted, based on the aerodynamic predictions. Studies at one of the most heavily used spring staging areas at Hvanneyri in western Iceland show rapid accumulation of body stores during the stopover period. Based on a caught sample and the use of field scores of abdominal profiles converted to mass, the geese increased body mass by at least 30g and 25 g per day during the mean 15-day staging period there. The total increase in body mass at this time was slightly less than that over the mid-December to mid-April period on the winter grounds. As in the case of the pre-migration period in Ireland, it remains to be demonstrated precisely what this increase in body mass equates to in terms of body constituents. Although there was some evidence that geese fed on adjacent wetlands, most of the increase observed in this study was sustained on the new green growth of cultivated grasslands. The three most common grass species showed differences in profitability because of leaf densities and nutritional quality, which affected rates of intake and hence accumulation of stores (Nyegaard et al. 2001). Individual geese show different patterns of exploitation of the three grass species. Therefore, there is the potential for density effects and social status to play a role in determining differential rates of individual nutrient acquisition on the staging areas, which could affect fitness. Because much of this rapid rate of body store accumulation is linked to green above ground plant production, it is therefore likely to be highly temperature dependent and likely to vary considerably with season. There is a need to assess whether there are differences in the rates of body mass accumulation between the birds feeding on traditional bog (mainly *Eriophorum angustifolium*) and sedge-meadow (mainly *Carex lyngbyei*) habitats and those studied on farmland. Furthermore, given the unusually large field size at Hvanneyri and the relative lack of disturbance, it is important to contrast the relative energetic costs and gains to a bird staging at this site versus other farms elsewhere in the staging range where disturbance rates are higher. This rapid rate of body store accumulation clearly makes this brief stop-over period more critical, in terms of balancing costs and gains, than other periods of the life cycle, and we need an adequate understanding of what factors affect nutrient acquisi-

tion during this critical time. All these factors need to be investigated and the results synthesised into a full appraisal of the conservation needs of the population. There remains a need to establish the simultaneous staging distribution of Greenland

White-fronted Geese in the lowlands of Iceland in order to establish the basis for a network of protected and sympathetically managed sites during this critical period.

5 Pre-nesting feeding

5.1 Introduction

Lack (1968) was the first to suggest that laying dates, clutch size and chick growth rates were co-adapted in birds to ensure maximum fitness. Laying date is important, since in most studied goose populations, goslings hatching earlier have a higher probability of survival and recruitment than those hatching later (e.g. Cooke et al. 1984, Warren 1990). Female geese in good body condition generally lay larger clutches and fledge more young than females in poorer condition (Ankney & MacInnes 1978, Ebbinge et al. 1982, Ebbinge 1989, Prop & Deerenberg 1991, Johnson & Sibly 1993, Warren 1994, Ebbinge & Spaans 1995). Hence, there is considerable evidence to support the idea that the ability of a female to accumulate nutrient stores at the earliest stage prior to the onset of breeding has a considerable influence on her ability to reproduce successfully in a given year.

For many years, it was considered that most arctic nesting geese built up stores on the wintering grounds, supplementing body condition at one or more staging area on spring migration before they reached the breeding areas. In the 1970s, the weight of evidence suggested that most arctic nesting geese bred immediately on arrival, or very shortly after arrival, on their northern breeding areas (generally as soon as nest sites were freed from snow cover). Therefore, it was naturally assumed that the internal nutrient stores remaining on arrival to the nesting grounds were of considerable importance in determining reproductive success (Barry 1962, Ryder 1970, Newton 1977, Ankney & MacInnes 1978). However, it has always been apparent that any supplement to the reserves of a female goose on arrival at the breeding grounds will maintain or improve her general nutrient status and increase her chances of reproductive success, as long as delay of first egg date after arrival carries no cost. Theoretical considerations suggested that, for the Lesser Snow Goose *Anser caerulescens caerulescens* at least, the fat stores available on arrival were only sufficient to account for 46-70% of the lipid and 14-55% of the protein requirements for clutches of 3-6 eggs (Meijer & Drent 1999). From this standpoint, female geese arriving at the breeding grounds have to supplement stores with substantial amounts

of dietary fat and protein in order to attempt reproduction at all.

As more studies have been carried out, it has become more apparent that few arctic nesting goose populations were truly capital breeders, in the sense that all reproductive material invested in clutches were derived from stores accumulated by the female in areas remote from the breeding areas. It is now widely recognised that many populations exploit spring staging areas close to, but not necessarily at, ultimate breeding sites and hence have the potential to supplement stores after the main spring migration and prior to first egg date. Raveling (1978) was amongst the first to recognise that many species of northern or arctic-nesting goose regularly nested 10-13 days after arrival on breeding areas, the period required for rapid yolk development. This enables the female goose to modify her timing of first egg date and the investment in her clutch based on external (e.g. weather, nest site availability, e.g. Carriere et al. 1999) and internal conditions (e.g. extent of stores, see Ganter & Cooke 1996).

It has since become clear that White-fronted Goose populations in particular rely upon pre-nesting feeding on the nesting grounds to supplement stores for investment in reproduction (Ely & Raveling 1989, Budeau et al. 1991). Other species show the same response (e.g. the Lesser Snow Goose, Ganter & Cooke 1996) including the very high arctic Greater Snow Goose *Anser caerulescens atlanticus*, thought originally to breed soon after arrival on the nesting areas (Choinière & Gauthier 1995).

5.2 Mechanisms for recouping body stores on the breeding grounds

Amongst the first studies to demonstrate prolonged pre-nesting feeding on the breeding grounds was that of the Greenland White-fronted Goose (MS1), where it was evident that geese fed locally for the period of at least 10 days between the first arrivals and the onset of breeding. Geese fed on the highly nutritious roots and stolons of *Puccinellia deschampsoides*, bulbils of *Triglochin palustre* and the lower stem of *Eriophorum angustifolium* and *Carex spp.*, excavated from low altitude

sandy substrates which were the first to thaw (MS1, Madsen & Fox 1981, Glahder 1999). These storage organs, relatively rich in carbohydrates and protein, were available to foraging geese long before the onset of green above ground primary production.

Once growth of such cyperacean plants starts, there is a rapid decline in absolute and relative quantities of storage polysaccharides and sugars (Shaver & Billings 1976) as well as nitrogen and phosphorous (specifically in *E. angustifolium*, Chapin et al. 1975). Hence, Greenland White-fronted Geese need to exploit this food resource immediately the thaw enables its extraction from the substrate, but before growth starts and quality rapidly declines. Climate change and the timing of migration therefore could have considerable implications for the ability of geese to exploit subterranean plant storage organs during the pre-nesting period (and potentially at other times of years also) as patterns of spring thaw become modified. Geese arriving too early are unable to extract plants from a frozen substrate, those arriving too late encounter food of diminished and declining quality.

With almost continuous daylight and the protection of their attendant gander, female geese fed for 68-82% of the 24 hour period on these high quality foods for 10-19 days prior to clutch initiation (MS1, Fox & Madsen 1981, Glahder 1999). The period required for rapid oocyte development in Alaskan White-fronted Geese *A.a.frontalis* is considered to be 11-14 days (Ely 1979). Hence, arriving geese are not only in a position potentially to modify first egg dates given arrival conditions, but also to accumulate substantial stores during this prelude to breeding.

5.3 Potential effects of differential staging within West Greenland

Based on studies undertaken in the southern part of the breeding range, satellite telemetry (MS20), observations of collared birds and other observations all suggest that arriving pairs tended to congregate in localised rich feeding areas which are the first to thaw (MS1, Glahder 1999). At such sites, there was an initial concentrated exploitation of feeding resources, where females fed for maximum uninterrupted periods and males gained some extra feeding time by association with groups of birds. Gradually, however, after

some 7 days, pairs split up and fed increasingly away from other birds, ultimately dispersing from the feeding aggregations close to ultimate nest sites, but still feeding on plant storage organs (MS20, Glahder 1999). In these situations, females increased their abdominal profile index from a median score of 1.5 to 2.5 between arrival on 4 May and 19 May, males increased from 1.0-2.0 over the same period (Glahder 1999). If the conversion factor determined from correlation of API and body mass in Iceland holds for the breeding grounds, this would represent an increase of 228 g and 285 g of body mass respectively prior to first egg date. Some of the increase in API amongst females will correspond to the increase in the size and extent of the ovaries and reproductive apparatus, hence in this case it is unlikely that all the increase in indices represents fat accumulation. Nevertheless, this field score supports the observation that this opportunity for pre-nesting feeding provided an important period of recuperation of used body stores.

Observations of collared birds moving within west Greenland in spring 1984 (MS3) showed geese may arrive and stage in one area and continue elsewhere for the remainder of the summer. Based upon the behaviour of the satellite birds, in 1997, 1998 and 1999, geese arrived in west Greenland between 3 and 17 May and staged at arrival sites between Kangerlussuaq (66°30'N) and northern Disko Bugt (69°50'N). Geese continued to their ultimate summer areas after an initial staging period of 9 days in 1998, but 16 days in 1999. One of the geese staged in the central part of the range before continuing to its summering area on Svartenhuk Peninsula in 1998, and similar patterns were witnessed in 1999, when the prolonged snow cover meant potential feeding and nesting areas in the north of the range were inaccessible well into June (MS20, MS23). It would therefore seem that in the favoured breeding habitat around Kangerlussuaq (66°30'N) and further north, the generally snow-free lowland wetlands offer a food resource to staging geese that breed locally and others that move northwards within the summering range (MS1, MS2, MS3, MS20, Glahder 1999, Glahder et al. submitted). It might be expected that these local breeding birds have access to earliest sources of food. However, as the population has expanded, so these birds will have faced increasing competition from the expansion in their own numbers and of those breeding further north that use the same spring staging areas. Glahder (1999) showed by combining satellite

imagery and searches in helicopters, that snow-free areas in west Greenland with suitable vegetation for staging White-fronted Geese were limited (c.28 important areas, with 8 supporting over 75% of all staging geese). Hence, there may be another density-dependent mechanism (partly dependent upon the pattern of thaw in each spring up the west coast of Greenland) which may restrict the ability of an individual to recoup its stores in readiness for investment in reproduction after the costs of migration from Iceland.

In seasons with a late thaw, geese staging in the region of 66-69°N but breeding further north face two alternatives. After initial refuelling they can move northwards into (possibly) unknown conditions or remain further south amongst higher densities of local breeders. In 1999, the thaw north of 69°N was greatly delayed. Geese flying northwards from staging areas would have encountered low temperatures and complete snow cover, resulting in lack of access to food and high thermoregulatory costs. In such a year, the northern summering portion of the population would be expected to breed with much lower success rate than those in the south, and this was certainly the case in 1999. The geese wintering at Islay (thought mainly to nest between 66 and 69°N) returned in autumn 1999 with 10.5% young (a below average production of young) but those wintering at Wexford (thought to summer largely north of 69°N) had the lowest level of production on record (5.5% young). It could be expected that, in late springs when snow reduces the availability of feeding sites throughout west Greenland, competition for limited resources in the immediate arrival period between 66-69°N could potentially result in a general reduction in breeding success in the population as a whole. Since nesting densities are still so low, and breeding habitat not obviously limited, it seems possible that spring staging habitat could be a factor restricting females from achieving breeding condition. This could be one limit to reproduction that would operate well before any density threshold is reached where nesting habitat *per se* restricts the number of pairs attempting to nest. It is rare that cold conditions prevail in the southern part of the breeding range and not in the north, so a further prediction may be that, despite highest breeding densities in the region of 66-69°N, the effect is likely to be increasingly manifest amongst the birds breeding in the north of the range.

5.4 Conclusions and discussion

We still know little about how Greenland White-fronted Geese acquire the resources to invest in reproduction on the nesting grounds after arrival from Iceland. Much more research is needed to determine the precise body condition of geese newly arrived from Iceland and the consequences of pre-nesting feeding and its contribution to a successful reproductive outcome. Arrival weights confirm that geese lose more weight (adult males c. 550 g and adult females c. 330 g based on arrival API converted to mass from Glahder 1999) on the 1,500 km passage from Iceland than over the same distance to Iceland from Ireland. However, this difference is in line with prediction given the need to climb up over 2,800 m to traverse the Greenland Ice Cap along the trajectory taken by satellite tagged individuals. There is a clear need to establish the precise mechanical costs of the flight over the Ice cap. We know birds congregate in favoured pre-nesting staging areas to recoup stores immediately on arrival. During this time, body mass (as calculated from changes in abdominal profile indices) increased at a similar rapid rate to that in Iceland in spring. Female geese, protected by attendant ganders, were able to exploit a rich feeding resource in the form of underground storage organs of plants during periods of uninterrupted foraging. Male were also able to increase body mass at a similar rate during this time due perhaps to daylight extending to 22 hours. Nest densities are generally low and nesting habitat apparently unlimited (see **chapter 6**). It therefore seems more likely that food supplies available at spring staging areas in the central part of the breeding range could limit the accumulation of stores to support reproduction rather than any resource associated with the nesting sites themselves. Because it appears that a substantial proportion of the entire population stages between 66 and 69° N, given a finite feeding resource available, increasing goose density at these staging areas may increasingly limit the number of geese attaining a level of body condition sufficient to permit successful breeding. It is predicted that the northern segment of the breeding population will not only face delayed timing of breeding by virtue of their nesting latitude and increasingly lower summer temperatures predicted from global climate change, but also the effects of greater goose densities on the southern spring staging areas.

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6 Reproduction

6.1 Breeding distribution and nest sites

The breeding distribution and biology of the Greenland White-fronted Goose has not been especially well described. The population is known to nest in low arctic tundra areas between 64° and 74° with greatest densities found between 66° and 68° N (Salomonsen 1950, Best & Higgs 1990, MS23, MS24). Nesting densities are generally lower than reported for other populations (<0.5 km⁻², maximum 0.28 km⁻², MS5, MS23, compared with 0.4-30 km⁻² in North America, MS5). There are no signs of territorial behaviour amongst studied birds, nesting pairs being widely dispersed as a result of the character of the available habitat (Stroud 1981a, MS24). First egg dates vary with season and latitude, but generally fall in the last week of May, being 20-28 May in Sarqaq dalen (70°06'N, Fencker 1950), 19 May - 17 June in Eqalummiut Nunaat (67°30'N, MS5). Nest site altitude in Eqalummiut Nunaat was influenced by availability of forage, determined by extent of snow cover and the phenology of the thaw. In 1984, a very late spring thaw commenced rapidly on 2 June when a warm föhn wind spectacularly thawed snow at all altitudes simultaneously. This was in considerable contrast to 1979 when there was little snow cover, but the thaw of the substrate progressed slowly up an altitudinal gradient. In 1979, nesting occurred early (mean clutch initiation 22 May 15 days after arrival, range 19-27 May) mostly at low altitude (below 300 m). In 1984, nesting occurred later (mean 11 June, 34 days after arrival, range 6-17 June) and more often above 400 m (MS1, Stroud 1981a, MS3, MS5). Nest sites are extremely hard to characterise, being distributed between sea level and 700 m altitude, but were predominantly on 1) slopes above marshes, 2) on or adjacent to marshes and 3) amongst hummocks adjacent to lakes (Stroud 1981a, MS5). Nests were almost exclusively near (invariably overlooking) *Eriophorum angustifolium* dominated marshes that in most cases formed the feeding area of the loosely attendant gander and the female during her recesses from incubation (Madson & Fox 1981, Stroud 1981b, 1982, MS5). Nest sites were generally in the hollow top of a hummock, or tucked between hummocks. There were no signs that nest site availability, access to feeding areas used during nesting, or breeding habi-

tat in general, were in any way likely to limit the numbers of birds nesting at that time.

6.2 Incubation

Incubation lasts 25-27 days, carried out by females only. Attendant Ganders feed on nearby marshes, both birds showed strong diurnal rhythms in alertness, feeding and roosting (Stroud 1981b, 1982, MS5). In 1979, the incubating female spent most time vigilant during the middle part of the day, sleeping in the early morning. In 1984, the female slept at midday and was most alert in the early morning. In 1979, four out of seven active located nests were unsuccessful and ultimately predated by Raven *Corvus corax* and/or Arctic Foxes *Alopex lagopus* (Fowles 1981). Foxes predated five of the six nests located in 1984, although such a high predation rate could relate to the presence of human observers (MS5). It is therefore not clear if these predation rates were in anyway typical of situations without human observers. It should be noted, however, that in spring, birds eggs (especially those of geese) comprised a significant proportion of the Arctic Fox diet, in the absence of other abundant prey items at that time (Birks & Penford 1990). In 1984, foxes were observed marking the positions of incubating White-fronted Geese on nests with scat marks, but seemed hesitant to attack sitting females, perhaps because of the risk of physical attack to the fox itself. Hence, the nest attentiveness of the incubating pair could play a critical role in determining predation rates. Nest defence by a female, joined by her mate from his nearby feeding marsh could see off a fox, but a nest where an absent female is feeding on a distant wetland could offer a fox an easy source of food. Among North American *A. a. frontalis*, groups of White-fronted Geese have been seen at nest sites and have joined in attacking foxes at nest sites known not to be their own (MS12). Such direct contributions to nest defence have not yet been reported from Greenland.

All forms of clutch defence necessitate the maximum attendance of the female at the nest, and here again, there appears a possibility for a condition-mediated impact on reproductive output.

A female with poor fat stores/reserves to maintain her through incubation will need to spend more time in feeding recesses away from the nest more often than one with greater fuel reserves. Recesses in 1979 lasted an average of 24 minutes, the majority between 19.00 and 01.00 hrs; on 20 June, the female left the nest twice in 24 hours but did not leave the nest again until 22 June when the clutch hatched (Stroud 1981b). Daily recess period increased from less than 20 minutes per day to 80 minutes as incubation progressed (Stroud 1981b), but the daily time spent incubating was still high (98.8%). The female would leave and fly towards the male, who would join her within seconds, the two birds flying to the feeding area. The male would stand alert close by the female whilst she drank and fed intensively; feeding was followed by bout of washing and preening before returning by a direct flight to the nest site. The male would stand within 20 m of the nest for the next 10-15 minutes before flying back to the marsh. The female spent some 20 minutes adjusting the nest, rolling the eggs and preening before settling to incubation (Stroud 1981b). The daily time spent incubating was high compared to Pacific Whitefronts *A. a. frontalis* (97.3%, Ely 1979) and Pink-footed Geese (96.2%, Inglis 1977), but less than Emperor Geese *A. canagius* (99.5%, Thompson & Raveling, 1987, Thompson in MS5). This may perhaps imply a greater reliance upon body stores to support the female through incubation than in other species, which supplement endogenous reserves by longer daily feeding recesses.

On hatching, young broods were escorted away from the nest site to feed on wetlands and marshes. In 1979, when nests were generally at low altitude, this involved substantial movement of broods from lowland areas up onto the plateau lakes, at distances of up to 5 km and 3-400 m uphill (MS5). In 1984, broods were hatched at higher elevations and did not move so far to nursery areas (MS5). Although there are no specific data on the relative predation rates in the two years, the distance over which parents must lead broods across an open terrestrial landscape from nest site to brood rearing habitats could affect the probability that newly hatched young fall prey to Arctic Fox and Raven.

6.3 Fledging to hatching

Mean brood size fell from 3.70 (n=10) in late July

to 3.46 (n=5) by fledging in early August in 1979 and from 4.25 (n=12) to 3.65 (n=20) in 1984. Parents were highly attentive to goslings at all times, while the goslings concentrated on feeding. Parents were observed brooding on a regular basis up to c.14 days after hatching, especially early on, for between 2 and 45 minutes per day, especially if the weather was cold or wet (Madsen 1981). Goslings were observed to run and seek shelter under parents in the first few days after hatch when a Raven flew over, but when larger, they would take to the safety of open water like their parents. Parents that nested at mid-altitude in 1979 immediately escorted their offspring up onto the plateau one or two days after hatching. In 1984, when the nests were constructed at higher elevations, broods had shorter journeys to get to the ultimate brood rearing nursery areas about the edge of plateau lakes. During brood rearing, parents fed for 35% of the time (42% amongst females, 26% amongst males), goslings for an average of 62% of the time, although the proportion of time spent feeding decreased gradually during the period to fledging (Madsen 1981). One gosling was observed for 3 hours without ever adopting the extreme head up posture typical of alertness behaviour. Parents with large broods spent proportionally more time vigilant than did parents of small broods or single goslings (Madsen 1981).

Non-breeders, which often moulted on the same lakes as breeders, were much less alert (although they associated in larger groups) and fed less than parents with young, which preened and rested less than the non-breeders. Non-breeders were not tolerated as close to broods as were other families (mean inter-distances 22m and 10 m respectively) and flying non-breeders were driven away from brood rearing areas by the parents. Attacks by breeders were more frequent on non-breeder groups than other broods and the attacking parents always won agonistic interactions even if the non-breeding groups were larger than the family flocks (Madsen 1981). On three different occasions, single associating non-breeders were tolerated at very close proximity to broods (Madsen 1981).

There are no currently available data relating to the condition of the adult female following incubation. As discussed later (**chapter 9**, Figure 9.4), following incubation, the female has invested in her clutch and incubated for an extended period characterised by very short feeding recesses. It is

predicted that at the end of this period of intensive investment, her body mass may well reach the lowest levels in the annual cycle (see Owen 1980, Figure 41). Potentially she will have depleted both stores (accumulated in advance of such investment) and reserves (body constituents not normally utilised to balance nutrient or energy budgets) during the period on the nest. Her survival is therefore highly likely to be influenced by her ability to regain adequate body condition in readiness for the wing moult. Since broods may be reared in habitats which offer the greatest abundance of the most suitable dietary items for gosling growth (for example high protein and energy content, low fibre but very small bite size), gosling nursery areas may not offer the best foraging opportunities to females to make good losses during incubation. Generally, this period in west Greenland is one of rapid plant growth, with locally abundant food resources and it is unlikely that there is a limit on the ability of brood females to make good such losses. Furthermore, there are no general indications amongst collared individuals of a high frequency of occurrence of widowed males returning to the wintering grounds with broods. Nevertheless, the ability of brood females to re-establish body condition from a particularly low level would repay study at this critical time.

6.4 Fledging to maturity

The period from fledging until departure from the summering areas has not yet been studied in any detail. Salomonsen (1950, 1967) described geese gathering into flocks and moving to lakes along the ice cap margin in continental west Greenland. Certainly geese are known to resort to heath areas in the interior at this time in the vicinity of Kangerlussuaq to feed intensively on berries prior to autumn migration (A. Reenberg, pers. comm.). This is an urgent research priority, since the accumulation of stores for the autumn migration to Iceland is a critical period in the annual life cycle about which nothing is known.

One pair observed throughout incubation in 1979 raised five goslings from six eggs of which four survived to reach Kintyre in Scotland (one gosling was shot in Iceland). In 1984, another observed pair raised six young from six eggs and although all were ringed, none have been subsequently recorded in Ireland or Britain. Mean brood size post fledging in Greenland in 1979 and

1984 fell from 3.46 and 3.65 respectively to 2.84 on the wintering areas in both years (based on mean brood size on Islay in both years in November, $n = 68$ and $n = 80$ for 1979 and 1984, MS5). Overall, 7% of goslings ringed in Greenland since 1979 have been shot and reported in Iceland on their first autumn passage to the wintering grounds. Annual survival of birds in their first year (i.e. from first to second winter 59.6%, 95% confidence limits 29.8%-89.5%) was significantly less than that of older birds (72.4%, 58.3-86.6% C.L. for the years 1984-1989, MS10), despite close association with parents in the first year (MS11). More recent analysis using a combination of ringing recoveries and capture-recapture analysis using resightings of collared birds gives a similar relationship (first-year weighted mean survival 67.8%, 63.2-72.0% C.L. versus 78.5%, 76.2-80.5% C.L. for adults, M. Frederiksen & A.D. Fox unpublished). Mean age at first pairing was 2.46 years (± 0.08 SE), age at first successful breeding 3.15 (± 0.17 SE) with no significant differences between the sexes (MS8).

6.5 Overall breeding success

The only regular long-term measure of breeding success comes from the wintering grounds, where the determination of mean family brood size and the proportions of young in the wintering flocks has been a regular feature of the monitoring programme for the population since 1982 (MS14, Fox et al. 1999). For some resorts, principally Islay and Wexford, the main Scottish and Irish wintering sites, these data are available since at least 1968. These indices of production underestimate true production. This is because they represent the numbers of young in the population after the impacts of autumn migration mortality. This includes hunting in Iceland, where it is known that juvenile birds are over-represented in the hunting bag of some 3,000 birds shot there annually in autumn (Wildlife Management Institute 1999, A. Sigfusson pers. comm.).

The annual production of young in the Greenland White-fronted Goose is positively correlated with average June temperatures (Zöckler & Lyсенко 2000). In 1992 (a late cold spring, with less than 10% young in the following autumn), 24 families were encountered during 2,538 km of flown transects counting geese on the breeding grounds. This compares with 83 during 3,298 km of aerial survey in 1995 (a mild spring followed by a warm

summer, with 20% young in Scotland – i.e. high production, Glahder 1999). However, this may not always be the case (e.g. production of similar numbers of young in the same study area in 1979 and 1984 despite a difference of almost a month in the timing of the spring thaw MS5). Furthermore, Greenland White-fronted Geese nest over an unusually broad range of latitudes so that, even within seasons, weather conditions in the southern parts of the range may differ widely from those in the north. Densities of families on the breeding grounds vary with the general levels of breeding success. The recent breeding survey of 1999 (a very late spring compared with most recent years) showed that by early June, conditions

on the breeding areas were good in the south of the range, but that deep snow conditions prevailed from Disko Bay northwards (MS23). The consequence may well have been that breeding birds in the north of the range abandoned attempts to nest altogether, since at Wexford (where the majority of birds originate from the north of the breeding range) geese returned with the lowest ever recorded proportion of young (chapter 5).

The proportions of young in the autumn population are generally lower than in most other populations of White-fronted Geese and other grey geese in the Western Palearctic (see Table 6.1). At

Table 6.1. Productivity data for Western Palearctic grey geese *Anser* spp. and for other populations of the circumpolar White-fronted Geese *Anser albifrons*.

Population	Mean % juveniles (time period for sample)	Mean brood size	Source
Taiga Bean Goose <i>Anser fabalis fabalis</i>	28.7 (1981-1989)	-	Madsen et al. (1999)
Tundra Bean Goose <i>Anser fabalis rossicus</i>	25.0 (1970-1994)	2.10	van Impe (1996)
Iceland Pink-footed Goose <i>Anser brachyrhynchus</i>	17.9 (1970-1995)	2.09	Madsen et al. (1999)
Svalbard Pink-footed Goose <i>Anser brachyrhynchus</i>	16.9 (1980-1995)	2.03	Madsen et al. (1999)
Iceland Greylag Goose <i>Anser anser</i>	17.7 (1970-1995)	2.24	Madsen et al. (1999)
Scottish Greylag Goose <i>Anser anser</i>	26.8 (1986-1997)	3.68	Madsen et al. (1999)

North American White-fronted Geese <i>Anser albifrons</i>			
Eastern Mid-Continent	33.3 (1979-1999)	1.67	US Fish & Wildlife Service (1999)
Western Mid-Continent	31.2 (1979-1999)	2.07	US Fish & Wildlife Service (1999)
Pacific	33.1 (1961-1999)	2.18	US Fish & Wildlife Service (1999)
Tule	26.2 (1986-1999)		US Fish & Wildlife Service (1999)

Western Palearctic White-fronted Geese <i>Anser albifrons</i>			
Zeeland, Netherlands	29.0 (1970-1994)	2.5	van Impe (1996)

Greenland White-fronted Geese <i>A. a. flavirostris</i>			
Wexford	16.3 (1968-1999)	3.41	this study
Islay	14.9 (1968-1999)	3.17	this study

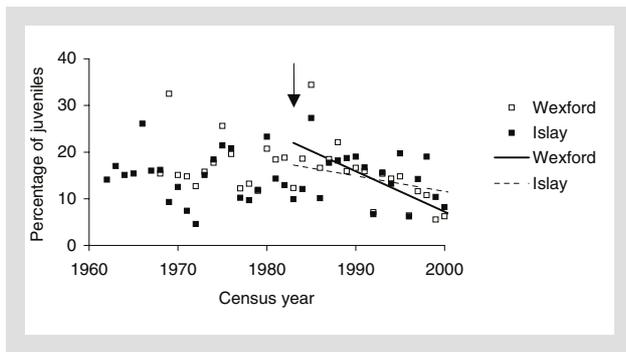


Figure 6.1. Annual breeding success of Greenland White-fronted Goose expressed as the proportion of juvenile birds in the wintering flocks at Wexford and on Islay for the years 1962-1999. Vertical arrow indicates the point at which hunting on the wintering grounds ceased (i.e. affecting both sites). Best fit least squares regression models are shown for both sites (as in following graph plots), the decline in proportion of young at Wexford since protection is statistically significant, although the decrease was not statistically significant for the trend on Islay⁴.

Wexford, the mean proportion of young for the years 1968-1999 inclusive was 16.3% (± 0.986 SE; range 5.5% in 1999 to 32.5% in 1969 data courtesy Oscar Merne, Dave Norriss, Alyn Walsh, Dúchas, The Heritage Service, National Parks & Wildlife, Ireland, Figure 6.1). On Islay for the years 1968-1999 inclusive it was 14.9% (± 0.945 SE; range 6.7% in 1992 to 27.3% in 1985 (data courtesy Malcolm Ogilvie, Greenland White-fronted Goose Study, Wildfowl and Wetlands Trust, Scottish Natural Heritage, Figure 6.1). Until recently, flocks at Wexford contained consistently higher proportions of young than at other resorts, and the same is true of the Islay birds compared to flocks in the

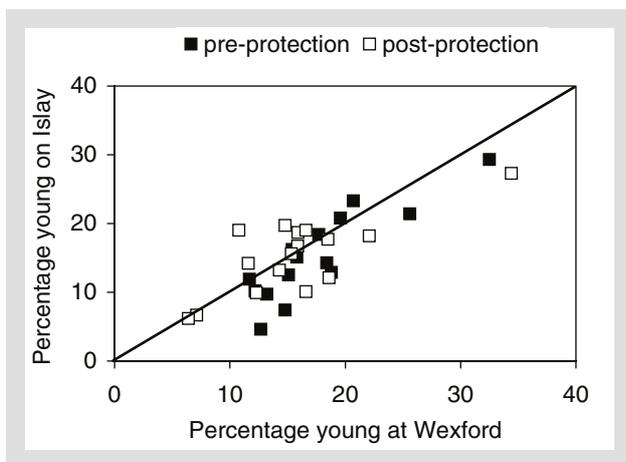


Figure 6.2. Patterns of annual breeding success (expressed as percentage juveniles in the winter flocks) at Wexford and on Islay for the period 1968-1999. The diagonal line signifies the line of equal production.

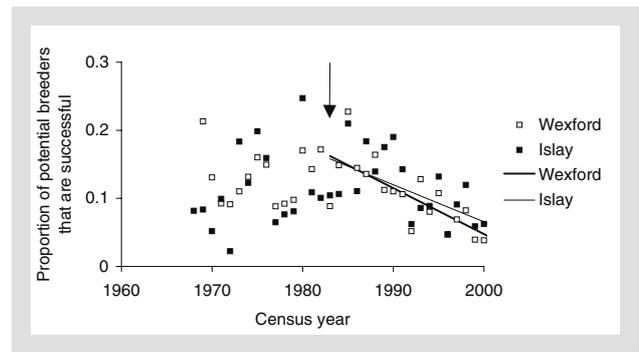


Figure 6.3. The proportion of potentially breeding adult females (assuming birds could potentially breed in their second summer) amongst the wintering flocks on Islay and Wexford that have returned annually with young during the period 1968-1999. The vertical arrow indicates the point at which the population was protected from hunting on the wintering grounds (i.e. at both sites). There have been statistically significant declines in these proportions at both sites since protection⁵.

rest of Britain (Pettifor et al. 1999). Overall, the annual patterns of breeding success are highly correlated between winter resorts (e.g. Figure 6.2). Poor seasons are associated with late spring thaw where thick snow cover in northern areas leads to abandonment of breeding (e.g. 5.5% at Wexford in 1999) or early snow in July which may affect gosling survival (e.g. 6.4% at Wexford in 1996). The relatively low percentage of young, returning in relatively large family units (see comparisons in Table 6.1 above), means that far fewer Greenland White-fronted Geese of potentially reproductive age return with young to the winter areas than is the case in other Whitefront populations. Whether this is the result of geese attempting to breed but failing, or simply not attempting to breed is central to understanding why recruitment is relatively low in this population.

There has been a significant decline in the overall breeding success amongst the population wintering at Wexford since protection, although there was no significant trend on Islay (see Figure 6.1). If it is assumed that birds can breed in their second summer (although there is little evidence that many do) there has been a significant decline in the proportions of those birds of potential breeding age which return to the wintering grounds with young at both major resorts (Figure 6.3). Hence, amongst both of the two major wintering aggregations (Wexford and Islay), there has been a decline in the proportion of potentially fecund birds that reproduce successfully since 1982. Pro-

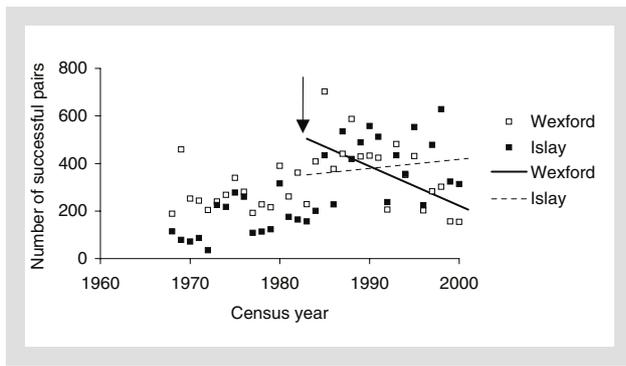


Figure 6.4. The annual number of pairs of Greenland White-fronted Goose returning to Wexford and Islay with young from the breeding grounds during the years 1968-1999. Estimates are based upon the numbers of young divided by the mean brood size. The vertical arrow indicates the point at which the population was protected from hunting on the wintering grounds (i.e. at both sites). There has been statistically significant decline in the number of successful pairs returning to Wexford since protection, although there was no statistically significant trend on Islay⁶.

ductivity of other wintering flocks away from these two major resorts is generally lower. Because these two sites have held 57-63% of the world population in the last 3 years, this has doubtless contributed to the general reduction in the rate of increase in the overall population. Since protection, the absolute number of successful breeding pairs returning to the winter grounds has increased on Islay (although not significantly) and has declined significantly at Wexford (Figure 6.4). The result is that the size of the combined

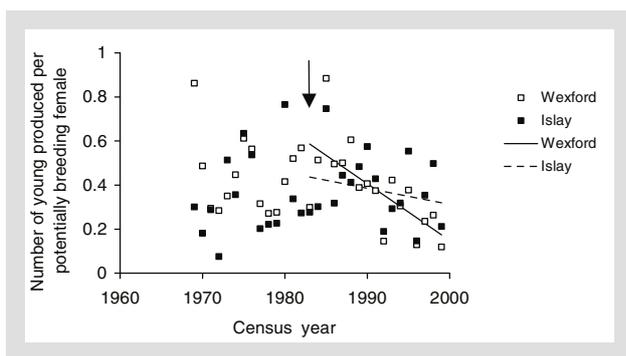


Figure 6.5. Annual production of young per potentially breeding female for the period 1968-1999 based on determinations on the wintering grounds at Wexford and Islay. The vertical arrow indicates the point at which the population was protected from hunting on the wintering grounds (i.e. at both sites). There has been statistically significant decline in this measure amongst geese returning to Wexford since protection, but the decrease was not statistically significant for the trend on Islay⁷.

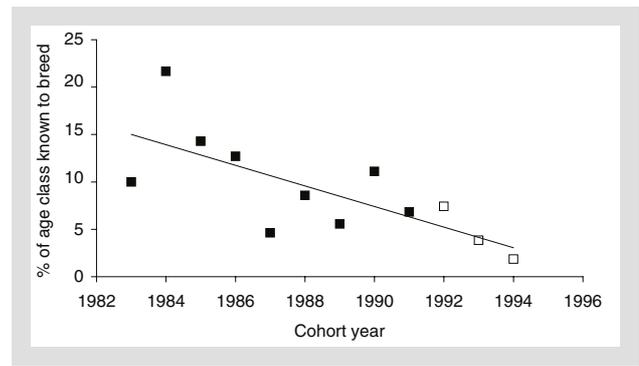


Figure 6.6. The proportion of each age class of goslings captured and marked in their first winter at Wexford and known to have survived to breed successfully since ringing commenced in 1983. Note that there are still several surviving birds from cohorts hatched since 1992 that have yet to breed and could recruit in future years. The decline is significant, but without the cohorts 1992-1994 inclusive, the trend is not significant⁸.

successful breeding population amongst 60% of the entire subspecies has remained remarkably similar (just under 1000 successful pairs in most years, excepting summers with cold weather conditions, Figure 9.3), despite the overall increase in the population as a whole. The consequence has been a reduction in the number of young produced annually per female of reproductively active age, although this decline is not statistically significant on Islay (Figure 6.5).

Amongst the sample of marked individuals, there has been a significant long-term decline in the proportion of ringed cohorts of young Wexford birds that survive and breed at least once (Figure 6.6). There was also an increase in the mean age of first breeding after 1988 amongst cohorts of birds marked as juveniles at Wexford in their first winter (Figure 6.7). Reductions again since 1992 are partly due to surviving birds from these cohorts failing to recruit to the present time. There has been no apparent change in the age of first pairing amongst these age classes during the period. This tends to suggest some density dependent mechanism may be operating at some stage of the life cycle. This increasingly precludes young recruits from entering the breeding class and reduces the numbers of birds of potential breeding status attaining that status in any one year. Although interpretation of such data is limited because of the delayed age of first breeding in the population, it should be considered that only c.10% of birds collared as first winter birds survive to their 6th winter. Any belated recruitment

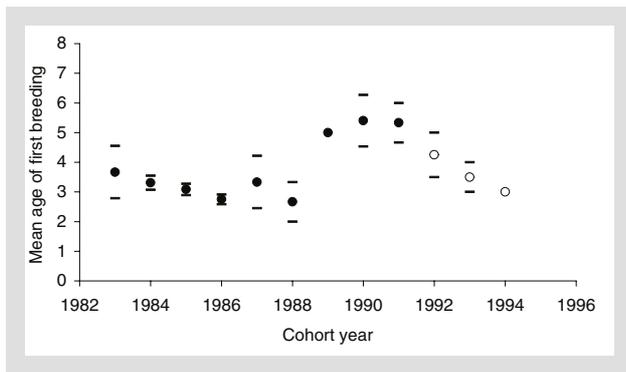


Figure 6.7. Mean age of first successful breeding (+ SE, determined by the return of an individual to the wintering grounds with at least one gosling) of goslings captured and marked in their first winter at Wexford since ringing commenced in 1983. Note that there are still several surviving birds from cohorts hatched since 1992 that have yet to breed and could yet recruit in future years, although these would only raise the mean age of first breeding for these latter cohorts.

of survivors of cohorts from 1988 onwards (Figure 6.7) will increase mean age at first breeding and make very little proportional difference to the proportions breeding shown in Figure 6.6.

Mean brood size amongst *flavirostris* has always been relatively high compared to other White-fronted Goose races, varying between 2.4 and 4.2 at both Wexford (mean 3.4 ± 0.07 SE) and Islay (mean 3.1 ± 0.07 SE) during the years 1968-1999. Mean brood size at Wexford was highly significantly correlated with proportion of young in winter, but there was no such relationship on Islay. There was a tendency for larger broods with increasing age of first breeding (MS8). This suggests that there could be some reproductive benefit to the individual from prolonged association with parents (in terms of production of young at their first breeding attempt). There has been a sudden increase in brood size amongst birds wintering on Islay in very recent seasons, despite no change in the observer or methods used to sample this parameter there (Figure 6.8). This has resulted in the mean brood size on Islay exceeding that at Wexford (generally always the converse until the mid-1990s, Figure 6.8). While in the 1970s and 1980s the productivity of the Wexford birds was nearly always greater than that of Islay wintering birds, in recent years this difference has reduced, and Islay productivity has in several recent years exceeded that at Wexford. Evidence for any density-dependent relationship for productivity was weak amongst the Scottish wintering flocks (Pettifor et al. 1999) and non-existent

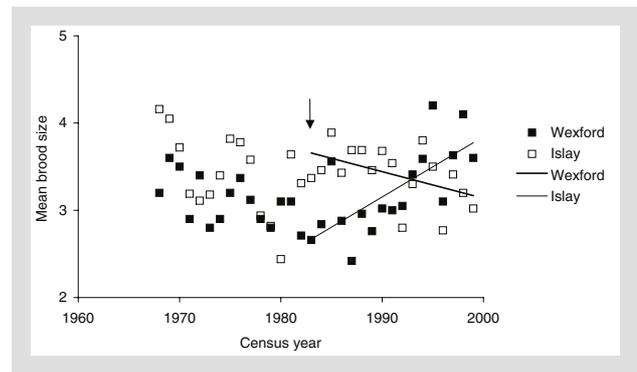


Figure 6.8. Mean annual brood size of Greenland White-fronted Geese returning to the two major wintering areas of Wexford and Islay. The vertical arrow indicates the point at which the population was protected from hunting on the wintering grounds (i.e. at both sites). The decline in brood size at Wexford since 1983 is statistically significant, as is the significant increase on Islay⁹.

amongst the Wexford wintering element of the population.

6.6 What does limit reproduction in this population?

We may be very encouraged that recent years have seen a huge increase in the basic descriptive knowledge relating to the breeding biology and ecology of Greenland White-fronted Geese. However, from a conservation point of view, all the descriptive information is useless if we are unable to identify and understand the processes involved. Direct comparisons with other White-fronted Goose races show that proportionally fewer *flavirostris* of potential breeding age return to the wintering areas with young. Yet when they do breed, they return with more juvenile geese per family than those of other races (see comparisons in Table 6.1). The implication is that the reproductive potential of the population is locked up in a small number of highly successful breeding pairs. The question therefore remains: why do so few females of breeding age return with young? And why is this number presently declining? Is it because of delayed pairing (and prolonged parent offspring associations) compared to other races (MS8, MS11)? Do offspring simply associate with parents and siblings because they can contribute to the reproductive output of kin and accumulate reproductive knowledge during a period when they have little prospect of breeding successfully? Or do they pair no later than

other races, but density dependent processes restrict the ability of young inexperienced birds to nest and incubate successfully? The increase in the age of first breeding in very recent years has contributed to the general decline in recruitment amongst marked cohorts of known age birds since 1984. Observations on the wintering grounds show that Greenland White-fronted Geese have a rigid social dominance hierarchy, so that a major determinant of an individuals' access to best feeding opportunities is the size of group with which it is associated (Boyd 1953). A young pair, abandoning the ties with parent-sibling groups (which may number up to 15 individuals in size) falls from a high-ranking group to a two-member group, with all the consequences for access to food and other resources that this behavioural change entails. Hence, the first step towards a reproductive attempt, that of obtaining a mate and accumulating appropriate stores for investment in successful reproduction, may carry a very heavy initial cost. The benefits of membership of large extended family units are found on the staging areas as well. In spring, family groupings maintained on the wintering grounds are perpetuated at staging areas in Iceland (MS27). Hence, at a number of stages in the life cycle, the decision to leave a family, form a pair and invest in a reproductive attempt may result in loss of access to best feeding opportunities at a number of points in the non-breeding periods of the annual cycle.

On the breeding areas, too, there may be advantages to existing parents of extended parent-offspring relationships. In another race of White-fronted Geese, central Canadian arctic *frontalis* young of previous years have been seen contribute to pre-nesting feeding alertness of potentially breeding pairs, and to remain in the vicinity of nest sites to assist with nest defence (MS12). In the absence of such 'helpers', new breeders may risk higher predation rates and hence impaired reproductive output for reasons other than experience. In terms of securing resources for the annual cycle of overwinter survival, spring migration and investment in reproduction, there would seem every advantage to remain with a group of kin, even for part of the year. However, as far as we know, this does not happen. Young birds leave family groups on pairing to embark upon a reproductive attempt as a lone pair. Hence, the low reproductive output of this population may in part relate to the behavioural consequences of flock structure, which creates a disincentive for

young birds to leave a large social group of related birds and attempt to 'set up home alone' as a lone pair. In other words, the high resource cost of leaving a family grouping favours delayed pairing relative to other races of the same species. Mature breeding pairs have the benefit of experience and the presence of associated offspring "helpers" from previous seasons. In contrast, inexperienced first time breeders (lacking associates) are likely to fail in the early stages of their reproductive lives. Furthermore, there could be some advantages to offspring in extended association with parents in gaining knowledge about successful reproductive techniques. This is supported by the fact that brood size increases with age at first breeding (MS8).

Given the continued increase in the numbers of geese wintering on Islay and the decline at Wexford, it is tempting to speculate that these differences in patterns of abundance are related to factors affecting the birds on the wintering areas. The extent of favoured feeding habitat has been reduced at Wexford in recent years, which could potentially affect the condition of departing birds and hence their reproductive success. There have been great changes in the extent and quality of grassland most favoured by the geese at Wexford Slobs in the last 14 years, and this has been reflected in the habitat use by collared geese at the site (Figure 6.9). Geese there increasingly use fodder beet provided as a sacrificial crop for longer

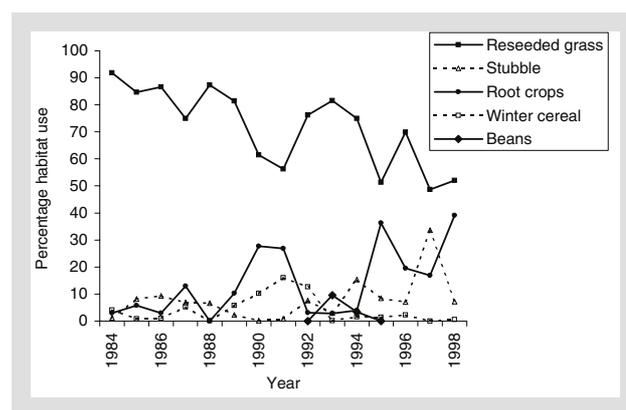


Figure 6.9. Proportion of different major habitat types used by wintering Greenland White-fronted Geese wintering at Wexford Slobs during the period 1984/85-1998/99. Data presented are based upon observations of collared birds only, since habitat type is recorded for every single field observation of these birds. There has been a significant decline in the use of grass and significant increase in the use of root crops (principally beet increasingly grown as a sacrificial crop for goose use at the site)¹⁰.

periods in each winter as the extent of suitable quality grass falls and tillage of former grassland areas (to produce crops largely unattractive to White-fronts such as linseed and maize) has increased. These changes in habitat use may have had nutritional consequences for the geese, which affect their propensity to breed, although there is no clear evidence of this from reduced API scores at departure in very recent years (see Figure 3.3).

Flocks of Greenland White-fronted Geese wintering at other sites in the south of the range are also showing the greatest declines in numbers in contrast to those in the north (MS14). Perhaps global climate change, or agricultural changes have in some way increased grass growth, especially in spring, in such a way that the timing of the nutritional early stages of growth no longer coincides with the pre-migratory fattening period of the White-fronts. Such arguments seem unlikely to provide a full explanation for what happens to birds 3,000 km away, given that the geese have 3 weeks to accumulate stores and reserves very rapidly in Iceland. Even after arrival in west Greenland, depending on the conditions encountered there, geese usually have a further period of 2-3 weeks feeding prior to initiation of nesting there.

Since patterns of winter segregation shows some relationship to those on the staging and breeding areas, it is equally, if not more likely that it is factors operating in Iceland and Greenland that are in some way restricting nutrient acquisition and hence recruitment. One major factor likely to affect geese (assuming a finite and constant food resource) is the increase in local bird density as a result of the recent expansion in numbers. Prior to protection, the birds using Islay and Wexford combined would have contributed some 6,400 non-breeding birds annually to the population as a whole. With the increase in overall numbers, the average number since 1982 has been 13,500 non-breeders. There are consequently more than double the numbers of geese summering in west Greenland than in previous years, and to these must be added the increasing numbers of Canada Geese colonising from North America. Some White-fronts show signs of moult migration northwards within Greenland, and the majority of the moult migrant Canada Geese were in the northern part of the breeding range of the Greenland White-fronted Goose. Hence, it seems likely that there may be increasing competition for food resources in the northern part of the range. There, the thaw has always been later (and therefore

productivity more variable dependent upon weather). The additional numbers of moult migrant non-breeders of both species could, however, have resulted in increased depletion of resources, perhaps at the cost of the number of successfully breeding birds in the area. To affect output, this density dependent effect would have to operate at pre-breeding feeding sites, either through direct interference competition for a finite resource or (in the case of food items taking more than one year to recover from exploitation) through a reduction in the overall food stock. Such an effect would be expected to be most manifest amongst the Wexford wintering birds, especially in seasons when the spring thaw was delayed, as has been increasingly the case in recent years. Hence, the overall decline in reproductive output may represent the combined effect of increasing numbers of geese and the result of the general cooling of the climate in western Greenland. This cooling has been occurring since the 1990s (Rigor et al. 2000) and is predicted by the various models of climate change to continue.

To distinguish between these two alternative explanations, we need to follow closely the behaviour and nutritional status of individual birds at every stage in their annual cycle. Although changes in fecundity have been documented, their proximate and ultimate causes remain obscure. What is important is that the population size and reproductive output should continue to be monitored in such a way that we can continue to follow the trends in population parameters and make some predictions about the likely trajectory of overall population size in the future. In this respect, it is important to understand factors affecting annual survival as well as fecundity, a subject considered in **chapter 8**.

6.7 Conclusions and discussion

Investment in reproduction in a long-lived animal represents a trade off between the availability of current resources, the cost of the reproduction attempt and the probability of surviving to breed again in a future year. It seems reasonable to assume that female condition determines the level of effort invested in reproduction, up to the point where the effort threatens her own future survival. In terms of initial investment, it appears that given the relatively long period of pre-nesting feeding in Greenland, clutch size decisions may be made by Whitefronts on the breeding ar-

eas (see Raveling 1978, Ganter & Cooke 1996) based on their own internal condition and the prevailing environmental conditions. This would involve assessment by the females of their ability to meet the nutritional demands of laying differing numbers of eggs and incubating the clutch given available stores and the supplement possible from exogenous food sources. Evidence is accumulating to suggest that exogenous sources supply much, or perhaps all of the fat needed for egg formation (Choinière & Gauthier 1995, Ganter & Cooke 1996, Meijer & Drent 1999). Hence, access to adequate food resources prior to first egg date may have a considerable impact on the ability of a bird to reproduce successfully.

We know little about female condition and its potential to affect reproductive success (before, during and after nesting), so the accumulation of knowledge relating to this parameter remains a priority. In particular, following body mass changes in particular individuals during the period from first arrival in west Greenland through to the end of incubation would be highly desirable. Tracking changes in body mass by capture and the use of balances under nests offers the opportunity to assess and contrast the potential of different individuals to successfully invest stores and reserves in reproductive attempts. Similarly, it is of great interest to understand more about how brood females recoup stores and reserves exploited during the laying and incubation period, a process about which we know nothing at present. Clearly behavioural adaptations (i.e. mechanisms resolving the conflict between self-maintenance and investment in brood protection) and dietary selection are both potentially involved, but could differ between individuals.

Despite the recent expansion in total population size, the absolute numbers of successfully breeding pairs returning with young to the two major wintering sites combined have been more or less constant, suggesting some density-dependent mechanism is operating on the breeding grounds which restricts recruitment. Amongst known age marked individuals at Wexford, the probability of recruitment has declined over time and the mean age of first breeding has increased from c.3 prior to 1988 to c.5 years of age in subsequent years.

Although difficult to measure in an objective way, the extent of breeding habitat available through-

out the summer range does not appear limiting. Nevertheless, the extent of habitat available in spring for pre-nesting feeding as well as later in the summer, are likely to vary with weather conditions, especially in the north. The Wexford geese breed mainly in the north of the breeding range, and the recent declines in fecundity of birds wintering at that site seem likely to be the result of conditions these birds encounter on their pre-breeding and nesting areas. Their migration to west Greenland differs little in distance or route from the Scottish wintering element of the population that breed further south. They could experience less access to energy-rich foods (such as barley and potatoes) in western than in southern Iceland, which could enable greater energy stores to be accumulated by predominantly Scottish birds staging in these Iceland lowlands (MS4, MS19). However, if it is exogenous energy derived on the breeding areas that represents a major determinant of clutch size or quality, early arrival to staging areas in southern Iceland (MS19) would give these birds an advantage over geese breeding further north. The latter would not only compete with local breeders in the staging areas of central west Greenland but also then migrate northwards within Greenland with a high probability of encountering severe weather conditions on arrival at ultimate nesting grounds. As goose densities have increased in recent years, it may be that all potentially breeding White-fronted Geese are encountering more competition for limited resources in spring, but the birds still needing to continue north face increased competition from non-breeders. As there is no further habitat to the north of the current range into which to expand, it might therefore be expected that geese breeding in the north of the range show greater density-dependent effects on the summering areas than those nesting further south. There is some evidence that this is the case; on Islay, the production of young per potentially breeding female has not declined significantly, the decline in successful breeding being compensated for to some extent by increases in mean brood size in very recent years. Increased mean brood size implies (i) adequate stores to lay large clutches, (ii) to incubate these successfully and (iii) to raise goslings to fledging. If the breeding range of the Islay-wintering birds has not changed, it is unlikely that their increased brood sizes have been brought about by change in habitat. Since their breeding area (mainly 66-69°N) is the area with greatest density of colonising breeding Canada

Geese, it might be expected that inter-specific interactions in this area would reduce reproductive output.

It may have been the case in the 1970s (prior to the period of population expansion by restriction of winter hunting) the northern breeders had an advantage over southern breeders. Staging further south on the summer grounds gave the opportunity to accumulate nutrient and energy stores remote from breeding areas, but still time arrival to nesting areas to optimise food availability there. This seems to be reflected in greater productivity amongst Wexford compared to Islay birds at that time (Figures 6.2 and 6.4). Subsequently, conditions of greater population size have increased local feeding densities in spring and substantially increased moult migrant non-breeder numbers using northern areas to regrow flight feathers. These changes in local density at key stages of the life cycle could potentially have turned the strategic advantage into an increasing disadvantage, especially at a time when a series of late springs has constrained the overall availability of early season food.

It seems likely that breeding habitat has not changed in extent, but that the quantity (and pos-

sibly the quality) of the resources available to females arriving in west Greenland have increased. Global climate models suggest there will be a short term and moderate warming of the central west Greenland coastal strip, whilst summer temperatures further north will be expected to fall. While increases in total population size may reduce overall access to finite food resources through competition, best quality individuals able to defend rich spring feeding areas could rapidly gain condition to invest in a clutch to be laid locally. Birds breeding further north face increased feeding competition, and poorer summer conditions later in the season on their own pre-nesting and breeding areas further north. Consequently, Wexford-wintering geese may be undergoing the very declines in fecundity predicted on the basis of climate change by Zöckler & Lysenko (2000), whilst Islay-wintering birds enjoy the positive benefits of this change. It would be interesting to analyse the historical meteorological archive to determine whether the difference in fecundity of these two elements of the population can be related to weather patterns in the north and south of the range. If not, there seem grounds for assessing in more detail the alternative explanations for these differences in breeding success in different elements of the population.

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7 Moult of flight feathers

7.1 Introduction

Considering the annual cycle of birds in the context of periods of nutritional stress, the period of replacement of the body plumage represents one such stage. The maintenance of plumage has considerable consequences for the individual, not just in terms of flight and aerodynamic efficiency, but also because feathers provide effective thermal insulation and, in the case of waterbirds, buoyancy. The Anatidae have evolved a pattern of replacement of feathers throughout the annual cycle, and indeed, ducks may have multiple plumages and moult throughout the year. In northern geese, replacement of feathers occurs throughout the annual cycle, except during the breeding period (e.g. Gates et al. 1993), although it is the period of flightlessness during the post-breeding phase which has attracted most research attention (Hohman et al. 1992).

In common with most of the Anatidae, and all northern-nesting geese, Greenland White-fronted Geese shed their flight feathers simultaneously and become flightless for a period of 3-4 weeks (Belman 1981). Flightlessness constrains feeding opportunities and denies flying as a means of predator escape, hence it seems highly likely that selection will have reduced the flightless period as much as food resources and predation risk would permit. Whether the flightless period represents a period of stress (i.e. where the nutrient demands of a bird exceed the supply derived from ingestion, resulting in catabolism of body tissue to meet that demand, *sensu* Ankney 1979) has been the subject of considerable debate (see Hohman et al. 1992). Hanson (1962) demonstrated that captive Canada Geese, fed *ad libitum* throughout wing moult, lost weight. Ankney (1979) pointed out that goslings increase their body weight 20 fold, grow leg and breast muscles and ossify a skeleton to almost adult size *and* grow a full set of body tail and flight feathers. Hence, he considered that it would be surprising if adult Lesser Snow Geese could not meet the nutrient demands of wing moult over the same time period. Nevertheless, Owen & Ogilvie (1979) showed significant declines in body mass with moult stage in Barnacle Geese in Svalbard amongst adult males and yearling females. Gates et al. (1993) demonstrated significant declines in

lipid reserves during wing moult in breeding females and non-breeding Canada Geese, suggesting that energy stores (i.e. nutrients accumulated in advance of periods of demand, *sensu* van der Meer & Piersma 1994) may be built up in advance of wing moult. Non-breeding Greylag Geese *Anser anser* moulting on the Danish island of Saltholm selected the most protein rich food available (Fox et al. 1998) and showed modifications to their nitrogen metabolism (Fox & Kahlert 1999), yet still lost 12-26% of their body weight (MS17). Subsequent dissection of birds obtained at this site throughout wing moult has shown that most of this involves use of extensive abdominal, mesenteric and sub-cutaneous fat deposits which are completely depleted by the time flight feathers are regrown (unpublished data). The study of van Eerden et al. (1998) also demonstrated that Greylag Geese moulting in the Netherlands could not meet their daily energetic requirements during moult. In combination with use of field scores of abdominal profiles to assess declines in fat stores (Owen 1981, Loonen et al. 1991), these authors concluded that geese relied upon fat deposits to meet their energy requirements during moult. Analysis of stable isotope ratios in the new grown feathers of the geese from Saltholm also suggest strongly that some of the protein involved in growth of feather tissue must originate from body stores accumulated prior to the moult period (unpublished data). Greylag Geese moulting in Iceland do not show significant changes in body mass during moult (A. Sigfusson & C. Mitchell in litt.), hence, it seems that this species shows a flexible response to nutrient acquisition and wing moult, depending on local conditions.

Is wing moult a period of energetic stress (*sensu* Ankney 1979) for the Greenland White-fronted Goose? What do the geese do during moult? What habitats are utilised? Are there any indications that the nutrient requirements of the period and finite habitat availability during this stage of the annual cycle could create density dependent limitations on the population in the future?

7.2 Moulting distribution and habitat

The non-breeding element of the Greenland White-fronted Goose population moults in close

proximity to the breeding birds. Since brood-rearing parents tend to be dominant over, and highly aggressive towards, non-breeders, at a local scale, non-breeders are often displaced from the favoured brood-rearing habitats. Salomonsen (1950, 1967) reported a northward moult migration of non-breeders, and there is no doubt that major non-breeding moulting aggregations lie well to the north of breeding areas where nesting densities are highest. Greenland White-fronted Geese were censused from the air in July 1992 and 1995 between 67°N and 72°N (Glahder 1999). This study located important concentrations of moulters (figures in brackets indicate numbers of birds counted from the air) on the Svartenhuk (72°N, 820-1,348) and Nuussuaq (70°N, 634-1,003) peninsulas, Disko Island (70°N, 855-1,788), Naternaq (68°N, 2,562-2,588), Eqalummiut Nunaat (67°N, 611-1,163) and Nasuttuup Nunaa (67°N, 1,387). Mean flock sizes tended to be highest in the north of the range, which supports Salomonsen's idea that there was some moult migration northwards. However, overall densities were low (<1 goose km⁻²) and varied considerably between areas and between years. In 1992, a cold spring and summer, more geese appeared to summer in the central areas (66°N-69°N), but 1995 was warmer than normal and geese were more numerous to the north and south (Glahder 1999).

Greenland White-fronted Geese characteristically use lakes during the flightless moult period (when they forage on peripheral wetlands and take to the safety of open water when threatened on land). The above-ground growth of the sedge *Carex rariflora* becomes dominant in the diet during the flightless period (Madsen & Fox 1981). *Carex rariflora* is characteristic of sedge meadows along rivers, about the margins of lakes and in other open flat areas where water lies for long periods during the melt. Such habitats were increasingly favoured by the geese and became the dominant habitat type during the early moult period (Madsen 1981, Madsen & Fox 1981, MS5). In Eqalummiut nunaat, during the latter part of incubation, the large non-breeding element of the population moved to high altitude to commence feeding about the lake margins of the plateau (MS6). Here, they initially exploited those flat or south-facing areas first to thaw, finally moving to forage on the snow patch vegetation on north-facing slopes that were the very last areas to initiate young green plant growth in the landscape. Hence, even at this altitude, the geese were able

to follow the phenology of plant growth by locally selecting between habitats.

Exploitation of such an altitudinal gradient is not possible at several lowland sites exploited by the geese in other parts of the range during the summer. One such site is Naternaq (68°N) where the geese moult on lakes that contain abundant suspended glacial sediment and so support rich emergent vegetation. Here the geese use emergent *Equisetum*, *Carex* and *Eriophorum* about the periphery of the pools. This open expanse of marine sediments exposed by isostatic uplift supports at least 2,600 breeding and moulting Greenland White-fronted Geese in a relatively small area. The geese exploit the numerous lakes and wetlands studded throughout a flat open plain composed of highly unstable fine glacial deposits. Further north, there are important concentrations in the Sullorsuaq and Kuusuat areas on Disko Island, where the very high mountainous terrain restricts the geese to coastal areas, vegetated outwash plains, vegetated valley bottoms and other lowland wetlands. The Disko Bay coastal strip northwards from Naternaq holds moulting birds at low densities, but high densities occur only in small pockets further northwards. The Nuussuaq peninsula is mostly high altitude and unsuitable for geese, but the valley north of Sarqaq (Sarqaqdalen where Fencker (1950) made the first ever studies of breeding Greenland White-fronted Geese) holds high breeding densities (Joensen & Preuss 1972). The high central valleys of Nuussuaq (300 m above sea level 70°N) have supported up to 1000 non-breeding moulters (Glahder 1999). These areas probably thaw too late to offer suitable habitat for breeding birds, but the delayed thaw postpones the early stages of plant production providing suitable nitrogen rich food in the early stages of growth during the moult. Further north, the terrain is very rugged and moulting geese are confined to discrete coastal lowland areas with suitable habitat, such as the extensive marshy lowlands of the Svartenhuk peninsula.

7.3 Do Greenland White-fronted Geese experience nutrient stress during moult?

In terms of the Ankney (1979) definition of stress, Greenland White-fronted Geese do not apparently show outward signs of nutritional stress during the moult period. Analysis of the body

mass at different stages of regrowth of flight feathers shows no significant decline in the mass of males or females during the flightless period (MS17). Average body mass was approximately 2.3 kg for females and 2.6 kg for males, close to the minimum average for both sexes amongst captured birds in winter (see **chapter 3**). This suggests that most of the geese still retain modest fat deposits throughout moult and are not approaching lean body mass at this time (i.e. that they retain some energetic reserve). The lack of any significant decline in body mass through the flightless period also suggests that, amongst the caught sample, there was no difficulty in obtaining necessary nutrients (particularly energy requirements and specific protein/amino acids) at these sites to sustain them through this period.

This pattern is similar to that found in other arctic nesting geese (e.g. Lesser Snow Geese and Brant, Ankney 1979, 1984, sympatric Greenland moulting Canada Geese MS17), in that geese retain little or no fat stores accumulated prior to moult for use during the flightless period. However, they show no decline in overall body mass whilst regrowing flight feathers. This is in contrast to the trends described for Greylag Geese on Saltholm and in the Netherlands (MS17, van Eerden et al. 1998), where 500-600 g of fat are apparently accumulated prior to this period. Why the difference? One reason could be access to food supply. In arctic situations, growth in plants is delayed relative to latitudes further south. Since the highest quality (particularly protein content) in above ground green parts of monocotyledonous plants is associated with the early stages of growth, it may be that food is simply of better nutrient quality. However, geese in moult sites above the Arctic Circle can also forage throughout the 24 hour period, punctuated by short pauses to rest, rather than showing a prolonged roosting period at 'night' (e.g. Barnacle and Pink-footed Geese, Madsen & Mortensen 1987, Greenland White-fronted Geese, Jarrett 1999). The interplay between nutrient absorption efficiency and food retention time has been demonstrated for geese (Prop & Vulink 1992). Hence, it would be most efficient for a foraging goose to 'eat little and often', filling the alimentary canal and resting for short periods to extend the digestive period. The alternative would be to spend prolonged periods with lower food retention times (i.e. with less efficient absorption of nutrients because of

high rates of throughput) and rest for a single prolonged period at night. That Greenland White-fronted Geese change from an essentially diurnal rhythm at other times during the summer (e.g. MS1, MS3, Madsen 1981, Stroud 1981b, 1982) to the continuous feed/rest pattern typical of the moult supports this argument.

Based on the historical capture data (MS17), it is tempting therefore to conclude that, given the ability to feed throughout the 24 hours of daylight, Greenland White-fronted Geese may be able to sustain their body weight without depleting reserves and complete moult without exploiting body stores. At present, we have no means of assessing the carrying capacity of habitats used for moulting by the geese and hence no opportunity to assess whether the current population is approaching the limit of moulting habitat available in west Greenland at the present time. However, the availability and quality of food resources during moult is certain to be dependent upon patterns of thaw, and there is no doubt that the timing of thaw varies considerably with season. In 1999, when there was deep snow covering all habitats down to sea level in early June north of 69°N, the extent of available moulting habitat was likely to have been much more restricted than in most years.

It is predicted that the climate in central west Greenland will become warmer in the very areas where the greatest densities of geese occur in summer (Zöckler & Lysenko 2000, MS23). If this proves to be the case, there may be a severe disruption to the phenology of thaw, which currently permits geese to exploit the early growth stages of different plant species following the sequence of their release from snow patch areas as a consequence of aspect and local topography. Locally, elevated temperatures may enhance plant production. If climate change results in all habitats in central west Greenland thawing earlier (especially at high altitude) the flightless moulting geese may 'miss' the best periods of above ground plant production if the geese are unable to modify their moult schedule. Conversely, the predicted cooling of summer temperatures in the north of the range could bring more summers with late snow lie, decreasing the extent of available moult habitat for birds using this region, and/or reducing local quality and quantity of the food supply.

7.4 Limits to suitable moulting habitat and potential inter-specific competition in the future

Since the mid-1980s, Greenland White-fronted Geese have faced a major change at their moulting sites. Canada Geese *Branta canadensis interior* have become established as a common breeding bird in areas of west Greenland previously only exploited by Greenland White-fronted Geese (MS13). Resightings and recoveries from ringed birds have shown that these geese winter in the eastern United States, from Massachusetts and Connecticut south to Delaware and probably originated from the Ungava Bay population of Canada Geese that breed in northern Quebec (MS22). The Canada Geese arrive in late May and commence nesting in habitats close to open water, so that there appears little competition in time and space for breeding habitat between this species and the Whitefront. However, during the moult, White-fronted and Canada Geese use the same habitats and areas to regrow flight feathers. At this time, both species are largely confined to areas within 50 m of open water. During this phase in the life cycle, increased nutrient demands and enhanced predation risk means there is an increased potential for direct competitive effects. In sympatric situations, the diet of White-fronted Geese showed high niche overlap with the colonising species and included higher levels of poor quality bryophytes than at moult sites from which Canadas were absent (Jarrett 1999, Kristiansen & Jarrett in Kristiansen 2001). Faecal analysis suggested that Canada Geese had a broad dietary range which changed little between sympatric and allopatric sites; in contrast, allopatric Whitefronts showed very narrow niche breadth scores based on faecal content, suggesting this species is a specialist grazer (Kristiansen 1997, Jarrett 1999, Kristiansen & Jarrett in Kristiansen 2001). It would therefore appear that Whitefronts coexisting with Canadas switched to a more generalised diet, perhaps in response to competition from Canada Geese for favoured food items. The two species appeared to segregate where they occurred together. In 45 agonistic interactions between the species, Canada Geese won on every occasion, even when outnumbered. As a consequence, Whitefronts would stop feeding and adopt alert postures when Canada Geese approached to within 3 metres (Jarrett 1999). In a study area in Isunngua, numbers of both White-fronted and Canada Geese increased from 1988, but in the mid 1990s, Greenland Whitefronts be-

gan to decline, and have disappeared as moulting birds from many lakes favoured in this area where Canada now predominate. The results from extensive studies are about to be published (Kristiansen & Jarrett in Kristiansen 2001). However, the implication from this study of a small area was that Whitefronts forced to moult with Canada Geese may be subject to exploitative competition as favoured plants are eaten out and interference competition when the dominant species physically prevent them from accessing potential feeding areas. Data from the 1999 aerial survey suggest that although both species showed highest densities in the same Kangerlussuaq region, at a local scale the two species were less likely to occur together than would be expected by chance (MS23). Whether this is a consequence of 'avoidance' competition or active exclusion remains conjecture.

7.5 Conclusions and discussion

The few studies of moulting Greenland White-fronted Geese suggest that these birds show no anticipatory accumulation of fat stores in preparation for moult. Rather, they shed and regrow flight feathers at their lowest level of annual body mass (equivalent to mid-winter minimum body mass). Since most studied northern and arctic geese show similar patterns, it is inferred that Greenland Whitefronts can derive all the necessary energy and protein required to complete the moult from exogenous sources. This suggests that under studied circumstances, moult habitat was not then limiting.

On the other hand, the confinement of moulting birds to the proximity of open water from which they can escape terrestrial predators inevitably constrains the amount of exploitable habitat available to flightless geese. This has been found to equate to a potential feeding zone of at most 150 m from water in other species (e.g. Madsen & Mortensen 1987, Kahlert et al. 1996) and possibly less than 50 m in Greenland Whitefronts (Kristiansen & Jarrett in Kristiansen 2001). This particular spatial limitation on foraging at this stage of the annual cycle suggests that this is a potential limitation on habitat availability on the summering areas.

In July, the moulting geese are confined to parts of the landscape adjacent to water bodies to which they can escape to evade predators. The amount

of available fresh green growth of graminoid plants with high protein at this time is limited in the landscape as a whole and dependent upon patterns of thaw. Global climate change could potentially interfere with the complex thaw gradients that ensure a sequence of protein rich food is available. Increases in White-fronted and Canada Goose numbers could also reduce available food resources to a level where nutrient avail-

ability could limit the numbers of moulting geese able to replace flight feathers on individual sites. Studies of moult, its precise physiology, the interplay between diet and behaviour need to be carried out in different parts of the range if we are to determine whether these various factors may limit nutrient acquisition and affect the population in due course.

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8 Survival

8.1 Introduction

Almost all goose populations have increased in the Western Palearctic in the last 45 years (Madsen et al. 1999). Since many of these are discrete and closed populations, the increases cannot be accounted for by immigration of individuals from elsewhere. These increases have not always been brought about by enhanced reproductive output, indeed for many populations, recruitment has actually fallen with increasing abundance (e.g. the Russian-breeding Barnacle Goose population Ebbing 1991, and see also **chapter 6**). Population modelling and simulation demonstrates that as relatively long-lived birds, northern nesting geese are sensitive to small changes in annual adult survival - very much larger changes in productivity rates are necessary to effect similar changes in the rate of population change (e.g. Tombre et al. 1997, Pettifor et al. 1999). The size of a population is determined by the relative annual gain (birth rate and immigration) balanced against loss (death and emigration), hence it is natural to accredit recent increases in abundance to declining mortality rates. As a very high proportion of individually marked geese has been recovered as a result of hunting, it is assumed that hunting is responsible for a high proportion of deaths (e.g. Ebbing 1991). Restrictions and complete banning of hunting on particular goose populations have resulted in immediate increases in some species including the Greenland White-fronted Goose (MS14). Others have shown less immediate responses after protective legislation (e.g. Russian Barnacle Geese Ebbing 1991 and Svalbard Barnacle Geese Owen & Black 1999). Others still have shown long-term increases despite apparent increasing mortality (e.g. Russian White-fronted Geese *Anser a. albifrons*, Mooij et al. 1999) or sudden rapid increases not linked in any way to changes in hunting restriction (e.g. the Iceland/Greenland Pink-footed Goose, Mitchell et al. 1999). Hence, while it has been suggested that increases in numbers of some goose populations are primarily due to the decreased mortality rates resulting from reduction in shooting, this is unlikely to be the sole factor influencing changes in population size. However, there is evidence that adult annual survival rates have been greater under protection than in earlier pe-

riods when the geese were subject to hunting exploitation (Ebbing 1991, MS14).

This relationship is important in order to understand the nature of hunting mortality if restriction on shooting kill is to be used justifiably as a management tool to achieve nature conservation management goals. It is necessary to understand the extent to which the number of deaths caused directly through hunting add to natural mortality (additive mortality), rather than being compensated for through a consequent reduction in natural loss through some density-dependent function (compensatory mortality, see discussion in Anderson & Burnham 1976, Nichols et al. 1984, Newton 1998). In order that hunting loss is directly compensated for by reductions in natural mortality, natural loss must already be density dependent and the kill cannot take place after the main period of natural loss. Hence the impact of the hunting bag in terms of the mortality in addition to natural loss depends on both the numbers killed in the hunt, the seasonal timing of both losses and the degree of density dependence involved in natural mortality. However, to demonstrate such a mechanism is important – if hunting mortality were completely compensatory, protection of a hunted population would not result in an increase of numbers. Conversely, demonstrating that mortality is completely additive enables restriction of hunting kill to be used as a tool to directly influence population size, controlling for reproduction rates. Hunting mortality may ultimately become partially additive to natural losses, i.e. at low levels, this would have no effect on the total annual death loss but above a certain density threshold, extra hunting mortality does contribute to a reduction in survival.

Serious declines in the numbers and range of the Greenland White-fronted Goose were attributed to habitat loss and the effects of hunting in the 1980s (Rutledge & Ogilvie 1979). This led to the protection of the population at most haunts on the wintering grounds and ultimately to the drafting of a management plan for the population (Stroud 1992). The geese had been legal quarry throughout its range (West Greenland breeding grounds, Iceland staging areas and wintering quarters in Britain and Ireland) until the early

1980s. They are now protected from hunting in Britain and Ireland (since 1982) and the season has been shortened to 16 August-30 April in Greenland (from 1985). Immediately following the implementation of protective legislation, numbers at the two most important wintering sites (Islay in the Inner Hebrides, SW Scotland and Wexford Slobs, SE Ireland) increased, suggesting that hunting was at least partially additive to overall natural losses. Observations of individually marked birds have shown that the population tends to be site loyal: only 14% of birds seen in consecutive winters changed site and 7% per annum showed permanent emigration (MS7, MS9, M. Frederickson unpublished data). Since hunting took place at both sites up to the time of protection, these cases offer an opportunity to explore the effects of changes in hunting legislation on the numbers using these sites. At Wexford, hunting was permitted again in the winters of 1985/86 and 1989/90. In this chapter, an attempt is made to determine the role hunting played in limiting numbers of Greenland White-fronted Geese at Wexford, using census data and reviewing various different approaches to the estimation of annual survival in this population.

8.2 Were annual adult rates of return to Wexford related to the size of the annual kill?

Counts of Greenland White-fronted Geese have been carried out at Islay and Wexford since at least the winter of 1967/68. Since 1982, carefully coordinated monthly counts have been carried out following a standard procedure at both sites (see Easterbee et al. 1990, Fox et al. 1994, MS14 for details). In years prior to this, up to 40 counts were carried out on Wexford Slobs in each winter, and at least two complete counts of Islay were undertaken annually. Large samples of birds have been aged in each autumn since 1968/69 to determine the proportions of first-winter birds present during early autumn or winter. It is important to understand whether the magnitude of the annual hunting kill was responsible for changes in the probability that a bird would return to either site in the following year.

Based on the annual maximum count from each winter (N) and proportion of juveniles in the population J for each winter t , an assessment of apparent annual adult return rate R_t for Wexford and Islay was determined as follows:

$$R_t = (N_t - J_t N_t) / N_{t-1} \quad (1)$$

This measure includes the net balance of immigration/emigration of individuals to each site as well as true survival between years. Furthermore, the measure suffers from sequential bias, in that an overestimation of apparent survival in year t is compensated for by an underestimation in year $t+1$. However, as far as the numbers of geese returning to the site is concerned, this measure has some utility in determining the way in which local abundance at a site varies over time. It seems likely that changes in annual immigration/emigration rates are relatively small, and probably relatively constant, so that annual adult rate of return to a wintering resort represents a proxy measure of annual adult survival. Is it possible to detect a change in annual adult return rate that can be related to the number of birds killed in any one year? Although not evidence of directly additive mortality, such change would support the argument that hunting at a known level has an impact upon the probability of a bird returning to a wintering site in a subsequent year.

At Wexford Slobs, the hunt was always limited in time and space, and the size of the bag determined for each year. Estimates of the numbers shot in Wexford Harbour were less precise, so annual totals killed there were estimated based on observations and discussions with wildfowlers in each season and these totals added to those killed at the Slobs. When the moratorium on shooting was lifted in 1985 and 1989, the bag was strictly limited and the numbers shot were recorded. In 1981/82-1983/84, a detailed study was undertaken to assess the level of mortality on the Wexford Slobs. Systematic (but not comprehensive) searches were carried out using a trained retriever dog on the Slobs and along the shores of Wexford harbour to find the bodies of unretrieved dead and dying geese. In 1981/82, when hunting took place, 28 geese were found in this way (in addition to the 142 reported shot), compared to none in following years with protection from shooting (D.W. Norris *in litt.*). For this reason, in all years when hunting occurred, an additional 20% was added to the known bag to allow for geese mortally wounded or not retrieved (based on general experience from many years and specific investigations during 1981/82). In this way, an annual kill was defined (K_t) for each year with hunting at Wexford. The number of birds killed K_t was then expressed as a proportion of the maximum numbers recorded N_t to give

the hunting mortality rate K_t for year t and plotted against adult annual return rate R_t for that season. Under the additive mortality hypothesis, it would be predicted that annual survival rate (and hence adult return rate) decreases with increasing kill rate in a linear fashion (away from $K = 1$ where the linear relation is a poor approximation, see Anderson & Burnham 1976). Under the hypothesis of completely compensatory mortality, annual return rate would be independent of variation in kill rate up to a threshold point where further increases in kill rate must result in reduced annual survival (Anderson & Burnham 1976). These two states represent extremes, with the slope b in the equation:

$$R = R_0 (1 - bK) \quad (2)$$

In this case R represents annual adult return rate and R_0 represents this measure when no hunting occurs. The slope b would be equal to unity in complete additive hunting mortality and zero over the range of realistic hunting kill rates in complete compensatory hunting mortality. Note that this analysis only considers compensatory mortality as this relates to winter hunting kill since, by definition, the term R_0 includes the hunting kill, which occurs in Iceland and Greenland, as well as 'natural' mortality. In this analysis, R is plotted directly against K and a regression model applied of the form:

$$R = R_0 - BK \quad (3)$$

The slope B was tested for significant differences from the predicted b values of 0 (perfect compensation) and $1/R_0$ (completely additive hunting mortality) using t tests.

The annual adult survival rate of Greenland White-fronted Geese wintering at Wexford was significantly negatively correlated with kill rate during the years 1970-1999 (Figure 8.1). This regression model explained more variance than the best quadratic fit. A quadratic fit would imply initial (i.e. partial) compensation to a threshold above which hunting mortality is totally additive. The slope did not differ significantly from the expected value of 1.129 (i.e. $1/R_0$, $t_{26} = 0.276$, $P > 0.05$), but was significantly different from zero ($t_{26} = 2.94$, $P < 0.01$). Mean apparent survival during the years with hunting (0.817 ± 0.021 SE) was significantly lower than in years without (0.884 ± 0.016 SE, $t_{26} = 2.48$, $P < 0.01$).

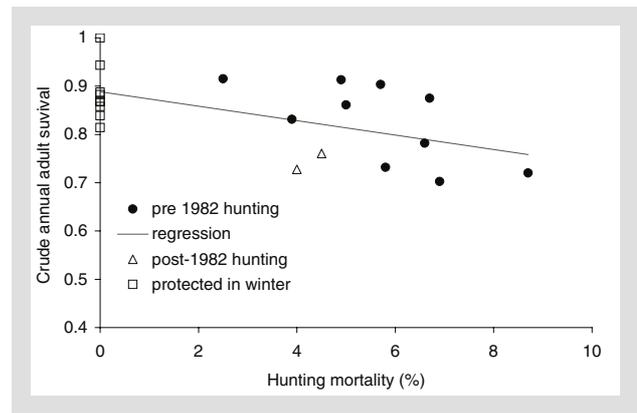


Figure 8.1. Plot of crude annual survival rate (based on adult return rates from annual census data – see text for full details) against hunting mortality rate (known bag plus 20% unretrieved losses expressed as a percentage of the peak winter count for each year). There was a statistically significant inverse correlation between these two measures¹¹.

It is clear that the annual adult return rate is not a good measure of survival rate, including as it does, the balance between immigration and emigration in the Wexford wintering population which is not a 'closed' one. However, these data do strongly suggest that the return rate was directly related to the size of the kill over the period that data are available, in a way that closely resembles additive mortality.

8.3 Modelling long term changes in annual adult return rates to Wexford assuming additive mortality

Given the low variation in the annual probability that a bird returns to winter at Wexford and the relationship between this property and annual hunting kill, it seems sensible to construct a very simple population model assuming constant annual adult return rate. In this way, given the observed numbers of young in each winter, it is possible to generate the expected numbers of adults in year $t+1$ based on total numbers in year t . The assumption is made that, for the Wexford wintering group of Greenland White-fronted Geese, (i) natural survival and (ii) the balance of between-year immigration and emigration are not year specific (i.e. in the absence of hunting, annual adult return rate is constant). In generating data for those years with hunting, it is further assumed that hunting mortality is completely additive, so that, in the years with hunting, annual adult return rate is the expected returning

number of birds less the hunting kill. Using only the initial maximum population count for the year 1967/68, and the mean apparent annual adult survival rate R_0 (derived from equation 3 above), the population size for each successive year $t+1$ was calculated as follows:

$$N_{t+1} = (R_0 N_t (1+J_{t+1})) - K_{t+1} \quad (4)$$

where K_{t+1} represents the hunting kill in year $t+1$, since maximum numbers usually occur at Wexford in mid winter after the finish of the hunt (MS9). We defined K_{t+1} as the number of geese recorded shot at Wexford Slobs and Harbour each winter plus 20% (see above). The model was then used to generate changes in population size given observed values for J_{t+1} up to 1999.

Substituting a constant annual apparent adult survival rate of 0.884 throughout in the simple deterministic model produced a remarkably good fit to the data until 1990 (Figure 8.2). Although apparently overestimating population size slightly in the early 1970s, the model shows good correspondence to the observed values during the period before and after hunting was banned at Wexford. After 1990, the model no longer describes the population development. As there has been no resumption of hunting in Ireland, this is not linked to shooting mortality on the wintering grounds. Rather, it is known from individual marking that 75% of the 1989 cohort of marked juveniles failed to return to the wintering grounds the following season, and adult mortality was also

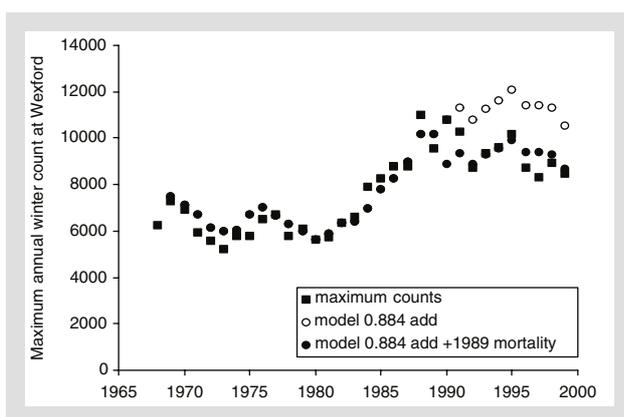


Figure 8.2. Model of changes in abundance of Greenland White-fronted Geese wintering at Wexford Slobs, based on constant annual adult rate of 0.884 (○), compared with the actual annual census counts for the years 1967/68-1998/99 (■). The outputs from the model incorporating the low survival of birds known from losses of collared individuals following the winter of 1988/89 are shown as ●. See text for full details.

10% higher that year (see next section). If the collared birds were representative of the wintering numbers at Wexford as a whole, this would have resulted in some 1900 fewer birds returning in winter 1990/91. If this exceptional loss is added in to the model, the fit is greatly improved (see Figure 8.2).

This approach is extremely simplistic and no attempt has been made to test goodness of fit of this model against alternative models. Nevertheless, the results underline the sensitivity of such long lived birds to small changes in annual survival/return rates. The simple model using a constant annual adult return rate (88.4% percent per annum) and the assumption of completely additive hunting mortality to the Wexford wintering site described the population changes extremely well in the period prior to and immediately following the cessation of hunting at this site. The anomalous deviation in very recent years appears to be at least partly explained by a year of very low survival, especially amongst juveniles, following the summer of 1990, known from population trends elsewhere and from lowered survival rates of neck-collared birds. There is thus reasonable evidence to suggest that hunting at Wexford may have been additive for the years 1970 to protection on the wintering grounds in 1982, and that the levels of kill experienced in that period resulted in no clear trend in numbers (MS14). However, with the cessation of hunting, Wexford numbers immediately increased, consistent with expectations if hunting mortality was additive at this site. Very recent stabilisation and slight declines in the numbers of geese wintering at Wexford are consistent with a high mortality event after winter 1989/90 and with observed declines in fecundity there (see chapter 6).

8.4 Current measures of annual survival rates based on individual histories

The first attempt to measure adult annual survival rates in Greenland White-fronted Geese was by Boyd (1958), using the Haldane (1955) method (as the numbers of geese ringed were not known). He estimated annual adult survival to be 66.1% (± 3.6 SE) based upon ringing recoveries of birds ringed and recovered (based largely on hunting returns) during 1946-1950. Subsequent analysis using similar methods for all recoveries from 1946-1974 found survival rates of 76.7% (± 3.4 SE, MS6). Both of these estimates were generated

during the period when the population was legal quarry in Greenland, Iceland, Ireland and Britain, although we have little idea of the precise size and distribution of the harvest at that time. By way of comparison, the survival rate for the period 1990-1997 (using only the recovery data generated from the collar-marking scheme) was analysed using the Haldane methods and gave an annual survival rate for the period of 81.7% (± 0.8 SE, H. Boyd, *in litt.*). The 5% difference in survival rate is very similar to the mean hunting mortality rate prior to protection (see Figure 8.1).

It was considered that the survival rate of Greenland White-fronted Geese prior to protection was too low to sustain the then level of hunting kill (e.g. Owen 1978). For that reason much bureaucratic and political effort was put into removing the subspecies from the quarry list, especially on the wintering grounds. As described earlier, this led to the effective protection of the population from hunting on the wintering areas from 1982 onwards (see MS14, Stroud 1992 and Fox et al. 1999 for full details). Evidence from counts of birds at a number of wintering sites strongly suggested that the increase in numbers that followed the cessation of winter hunting was due to the increase in return rate of birds, not to changes in reproductive success (MS14). Indeed, we are now aware that since protection, breeding success has actually decreased amongst the Wexford and Islay wintering elements of the population, which provides more evidence that restriction on hunting has increased annual survival.

There was no extensive visible marking programme in effect before and after the implementation of protection in winter. This would have allowed a more sensitive monitoring of changes in survival based on individual bird histories and thus enable the interpretation of subsequent changes in overall population size. The capture-mark-recapture study using neck-collared birds initiated in Ireland only commenced after protection had been implemented. Using the resightings of neck-collared birds marked at Wexford during 1984-1989, Bell et al. (MS10) calculated annual adult survival using SURGE4 models (Clobert et al. 1987, Pradel et al. 1990) to generate maximum likelihood estimates of 78.5% (± 1.4 SE). This compares with 72.4% (± 7.3 SE) based on ringing recoveries from the same ringing programme using BROWNIE (Brownie et al. 1985). Using the Haldane method on birds marked in the winter period gives a survival estimate of 72.1% (± 1.1

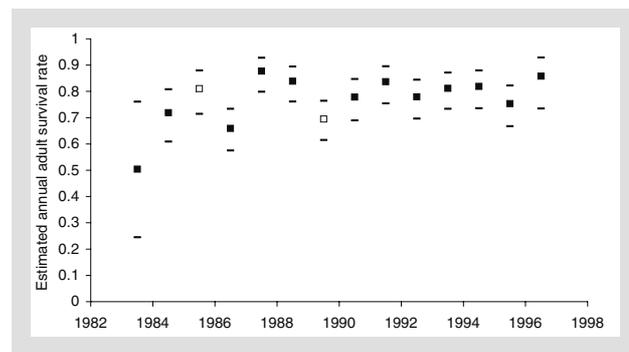


Figure 8.3. Annual adult survival rate ($\pm 95\%$ CL) for Greenland White-fronted Geese caught at Wexford, 1983/84-1997/98 based on observations and recoveries of neck-collared individuals using the MARK suite of programs (see text and Appendix 1 for details)¹². Open symbols indicate those seasons when the hunting season was opened at Wexford for a limited shoot. The unusually low survival estimate and large confidence intervals for 1983 probably reflect small sample sizes in that year.

SE) for the period 1984-1989 (H. Boyd *in litt.*) The SURGE models use much more fine-grained information and provide year- and age-specific maximum likelihood estimates, based on data-rich repeated resighting histories of individual birds. The Brownie techniques utilise the geese caught, ringed and never retrieved again to estimate reporting and recovery rates in a more sophisticated survival estimation than the Haldane method. It is not possible to use the Brownie et al. methods on the 1940s data, because some of the original capture and ringing data do not exist.

More recent analysis has been carried out using a combination of recoveries and resightings of collared birds at Wexford using MARK (White & Burnham 1999, based on the recovery-recapture models of Burnham 1993 and multi-stage models of Hestbeck et al. 1991). The selected model was one of survival, which varied with year independently for adults (weighted mean 78.5%, see Figure 8.3) and juveniles (67.8%, but which showed greater variability, Figure 8.4), with a mean of 7% permanent emigration per year (M. Fredriksen & A.D. Fox unpublished). There was no effect of hunting on annual adult or juvenile survival estimates in the two winters (1985/86 and 1989/90) when the moratorium was lifted at Wexford, although the survival rates in the year following 1989/90 were the lowest for adults and juveniles (Figures 8.3 and 8.4). In 1990/91, only 7 out of a marked cohort of 33 first winter juve-

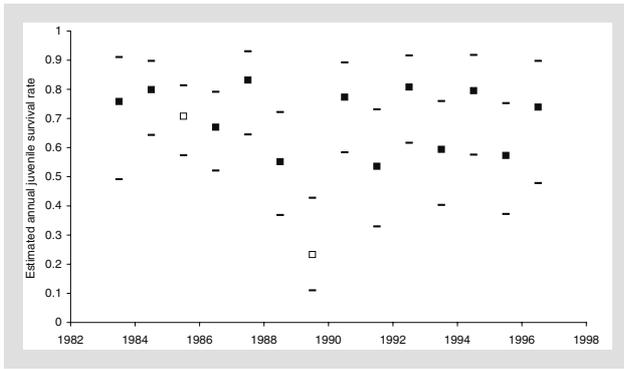


Figure 8.4. Annual juvenile survival rate (\pm 95% CL) for Greenland White-fronted Geese caught at Wexford, 1983/84-1997/98 based on observations and recoveries of neck-collared individuals using the MARK suite of programs (see text and Appendix 1 for details)¹². Open symbols indicate those seasons when the hunting season was opened at Wexford for a limited shoot. Note the unusually low survival rate of geese marked as goslings in 1988/89 that was not linked to hunting kill in that season.

niles marked in the previous winter were ever reported again, a remarkably low annual return rate (21%). One of them was reported from Pennsylvania, in the eastern United States in December 1990. It may be that the low survival rate that season was due to geese encountering severe weather (for example a storm in autumn 1990 that blew them westwards off track). The Lamb daily classification of weather systems over the British Isles for that period shows no obvious anomalies that could account for this extraordinary loss (H. Boyd. *in litt.*)

Based on these two years, there is no evidence from the probability of birds shifting from Wex-

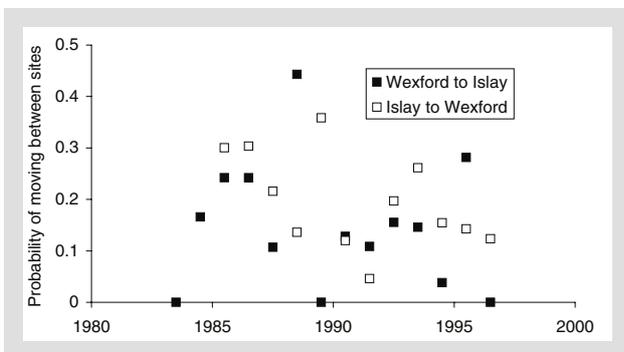


Figure 8.5. Transition probabilities for Greenland White-fronted Geese moving between Wexford and Islay and vice versa for each year from 1983/84-1997/98. There are no significant trends in the movement of individually marked birds over the period based on observations of neck-collared birds¹².

ford to Islay (e.g. Figure 8.5) or elsewhere, that Greenland White-fronted Geese were more likely to emigrate from Wexford in winters following those with an open shooting season. Hence, there is no evidence to suggest that the opening of the season in very recent years has had a demonstrable additive effect on annual adult survival rate or has enhanced emigration rate.

8.5 Conclusions and discussion

Ruttledge & Ogilvie (1979) suggested that the loss of peatland habitat might have concentrated Greenland White-fronted Geese into areas where they were easier to shoot. Not only would this have had an adverse effect on survival rates, but it would also have made them more sensitive to hunting disturbance. Human disturbance in general has since been shown to have a major influence on the size and trends in numbers of several flocks (Norris & Wilson 1988, 1993, MS14). In former times, the bogs and moorlands they exploited would have provided food, daytime resting areas and nighttime roosts all with very little disturbance. It would therefore seem likely that the extensive historical loss of such feeding sites for wintering flocks and increasing levels of disturbance, reduced their ability to acquire necessary stores to survive and reproduce at that time. It does seem likely that habitat loss in such a site-faithful population made it more vulnerable to hunting and disturbance. Since hunting does appear to have a direct depressing effect on overall survival rate, it seems more likely that increased susceptibility to hunting (prior to the 1980s) caused the declines and extinctions that occurred then. Nevertheless, reduction in breeding output through failure to accumulate sufficient body stores could also have resulted from the increased disturbance experienced at unfamiliar wintering sites. However, we shall never know precisely how changes in habitat availability affected the demography of the population and caused the changes in local wintering numbers at specific sites.

There is no doubt, however, that despite continued loss of traditional peatland feeding areas during the latter part of the 20th Century, the Greenland White-fronted Goose proved itself as able as other grey geese to exploit new and novel agricultural habitats. Flocks initially moved to rough pastures and flooded grassland, but latterly have also exploited intensively managed grass-

lands. This process was certainly underway when the geese began to exploit the newly created Sloblands in Wexford Harbour (probably at or around 1910, Ruttledge & Ogilvie 1979), despite the complete absence of boglands in the vicinity.

Despite their traditional habitat and high winter site fidelity, these geese have shown an ability to exploit new habitat opportunities. That said, only one flock of White-fronted Geese is known to have colonised and established an entirely new wintering site since 1982. The process of exploiting grassland habitats, either those that are seminatural or of low intensity agriculture, has continued to the present day. Although many flocks still resort to peatland habitats to feed and sleep at night, there are few flocks remaining that exploit bogs by day (MS14, MS24). Norriss & Wilson (1993) argued that this transition to more agricultural grassland was not forced upon the geese by habitat loss in very recent times, but that the geese responded to the creation of more profitable feeding habitats without loss of traditional ones. This change has been occurring gradually since the 1950s, and therefore does not coincide with the dramatic increase in numbers that has occurred since protection from hunting. Hence, while it is possible to argue that increases in total numbers since the 1970s have been associated with increasing use made by the population of more intensively managed farmland, this cannot be anything more than a contributory factor enabling contemporary increase, rather than the specific cause. This is further supported by the fact that the population range has effectively remained the same in the last 20 years, although several winter flocks have disappeared.

This ability to adapt to the exploitation of new habitats may be linked to the availability of such habitats in the neighbourhood of traditional flock ranges. In areas of Scotland where extensive areas of intensively managed grassland are available (e.g. Islay, Kintyre, Stranraer), Greenland White-fronted Geese have switched to these whilst retaining traditional roosts. This process has presumably run in parallel with improving grassland management practices since the early 1960s. In areas with little intensive grassland management and no tillage (e.g. many of the Hebridean islands such as Jura, Mull, Skye and Lewis) flocks remain small (see land use classification maps in Mackey et al. 1998). Equally, in areas with suitable extensive arable and managed grassland but no traditionally used roosts, the

species is totally absent (e.g. in Ayrshire and large areas of Dumfries). However, flocks with wintering areas with the greatest area of improved grassland within traditionally used areas have tended to show increases in their number. This is in contrast to those flocks where land use has changed little, or agricultural land has been abandoned. In this way, there appears some fitness consequences to the availability of managed grassland which affects the rate of change in local wintering numbers, although it is far from clear if these relate to annual adult survival, reproduction or rates of immigration/emigration. Investigations of these parameters in relation to habitat and individual quality remain a priority for future research.

In contrast, it would appear from the evidence presented here and in MS14 that, prior to protection, the numbers of birds wintering at Wexford and Islay were limited prior to protection by the numbers shot. These two sites have held some 60% of the population since protection, hence this limitation was a significant one. There are no accurate collated hunting statistics for Islay. Since protection on the wintering grounds in 1982, the return rate of birds to Wexford and Islay has been more or less constant. At Wexford, incorporating the numbers killed into a simple model suggests that the return rate has not changed since the late 1960s. Hence the product of annual survival and emigration/immigration balance has remained constant at around 88.4% over 3 decades of large-scale land-use change. The relative stable numbers during 1968-1982 seem to have been due to the balance between hunting off-take and changes in annual breeding success. Immediately after protection, numbers increased consistent with the same probability of annual return rate. In the absence of the hunt, this resulted in the increased numbers. The increase has continued at rates regulated by the potential of reproduction to replace lost individuals.

Since the start of the 1990s, the numbers wintering at Wexford have shown signs of decline due to falling fecundity (**chapter 6**) and to catastrophic losses of young and their parents in 1990, hence declines in reproduction appear now to be limiting the numbers at Wexford. Since the reduction in fecundity is mirrored amongst the wintering numbers on Islay and perhaps other wintering areas as well, this seems to be a general phenomenon in the population as whole in recent years. On Islay, the reduction in reproduction rate has

not yet been sufficient to halt the linear annual increase in numbers since protection.

The Greenland White-fronted Goose was a population that was declining due to habitat loss and hunting, but where protection from hunting has increased survival in proportion to the former size of the hunting bag, enabling the population to enter a phase of increase. Apparently confined to

traditional areas by behavioural site loyalty throughout its range, the population has shown signs of slowing its expansion in numbers in very recent years due to declining reproductive success.

9 Synthesis

9.1 Anticipatory acquisition of nutrients, density dependence and constraints upon fitness

In spring, every female Greenland White-fronted Goose of breeding age must clear three nutritional hurdles in order to breed successfully. The annual cycle involves completion of two spring migration episodes. Both require the bird to make the necessary physiological and anatomical modifications and lay down fuel reserves to sustain two flights of 1,500 km, one over the sea to Iceland, and the second crossing the sea and the Greenland Ice Cap. The ease with which an individual can clear these hurdles has various fitness consequences. Failure to construct large enough flight muscles or energy stores to sustain the flight will result in death *en route* – this much natural selection will ensure. However, the ability to accumulate the necessary resources to only just complete the two flights leaves no stores for investment in reproduction. Slow accumulation of adequate stores will delay departure from staging areas and

time of arrival to the nesting grounds, so condition mediated timing of breeding may also affect reproductive output in this way. To complete the journey to the breeding grounds early enough with some extra stores remaining is likely to contribute to the investment in reproduction, and this, together with efficiency in finding food during the pre-nesting period, is likely to determine, to a major extent, the reproductive success of that individual.

On the other hand, there must be some upper limit on the amount of energy or other nutrient stores, set by the cost of carrying such excess body mass (e.g. predation risk and enhanced energy use induced by heavier flying weight, see review in Witter & Cuthill 1993). Nevertheless, the ability to acquire specific nutrients to store for use at key points in the winter and spring has consequences for the ability of a bird to reproduce, or, in the extreme, to survive each migration. The efficiency (and therefore the rate) of accumulation of such 'capital' through a series of acquisi-

Table 9.1. Protein and lipid energy requirements for a laying Greenland White-fronted Goose, her clutch of 3 or 6 eggs and subsequent incubation. Analysis follows methods of Meijer & Drent (1999), using Basal Metabolic Rate estimated from the relationships for non-passerines derived by Aschoff & Pohl (1970), i.e. $BMR = 330.W^{0.722}$ (where W = body weight in kg.) and based on the assumption that daily energy expenditure (DEE) during laying is equivalent to $1.7 \times BMR$. Protein costs were calculated using the modified formula of Robbins (1981) related to body weight according to the formula $2.68.W^{0.75}$ g protein day⁻¹ (see Meijer & Drent 1999 for full explanation).

Lipid costs of egg laying and incubation								
Costs	♀ body mass (kg)	BMR (kJ)	Lipid equivalent of 1xBMR (g/day)	DEE (xBMR)	Laying/incubation period (days)	Lipid used in laying/incubation period (g)	Lipid used in clutch (g)	Total minimum and minimum lipid investment (g)
Laying	2.78	690	18.2	1.7	4-8	123.5-247.1	49-98	172.5-345.1
Incubation	2.78	690	18.2	1.1	26	519.6		519.6
Protein costs of egg-laying and incubation								
Costs	♀ body mass (kg)	Maintenance protein (g/day)	Laying/incubation period (days)	Protein used in laying/incubation period (g)	Protein used in clutch (g)	Total minimum and minimum protein investment (g)		
Laying	2.78	5.7	4-8	23.1-46.2	56-112	79.1-158.2		
Incubation	2.78	5.7	26	165.0		165.0		

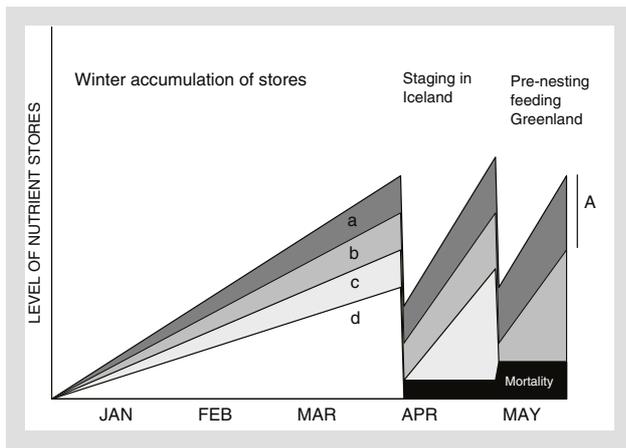


Figure 9.1. Patterns of theoretical accumulation of stores by adult female Greenland White-fronted Geese during the first 5 months of the year. Trajectories represent 4 different individuals that differ in their rate of accumulation of stores (because of feeding efficiency, behavioural dominance, parasite load, etc.). If birds fail to accumulate sufficient reserves to reach a particular threshold at winter departure, they may fail to reach Iceland (individual 'd'), or do so with insufficient stores and too little time to accumulate stores to complete the journey to the west coast of Greenland (individual 'c'). Even if accumulated stores are sufficient to support the flight successfully to the breeding areas, the individual 'b' still cannot accumulate stores rapidly enough post-arrival to the level required to initiate a clutch (shown by 'A' above), hence she incurs a fitness cost in terms of failed breeding. There will be a range of breeding options available to the female dependent upon the level of energetic reserves at the commencement of breeding. Hence, within the band "A" the timing and extent of nutrient acquisition will affect reproductive investment through factors such as manipulation of first egg date or clutch size. It is also possible that birds arriving in Greenland and acquiring sufficient nutrients on the pre-nesting areas to invest in a clutch may potentially affect the relative quality of her investment. This has consequences for her reproductive output (in terms of her egg size, clutch size, incubation constancy, etc.). Seen in this way, small differences in feeding efficiency, and hence accumulation of stores, can be seen to have a cumulative effect during the five or so months before first egg date. This is why the sward type a bird feeds upon, or the feeding efficiency of an individual, or the level occupied by the individual in a dominance hierarchy may have such consequences in terms of fitness measures. Note also that the critical periods of store acquisition are those in Iceland and Greenland, where rates of accumulation are most rapid and therefore where small perturbations are likely to have most effect. Note also however, that even during the slow accumulation of stores on the wintering grounds, failure to accumulate stores bears a future cost, insofar as the short episodes of rapid store accumulation in Iceland and Greenland do not permit individuals to 'catch-up lost ground' at these later stages in the spring period.

tion and depletion events has therefore the potential to influence the fitness of individuals.

Let us assume that we can use body mass as currency to reflect the 'adequacy' of stores accumulated by an individual to complete migration to Iceland and onwards to Greenland. In this way, we can diagrammatically represent the mass trajectories of individuals which exhibit different rates of accumulation of such stores under the same environmental conditions (Figure 9.1). Body mass may in reality represent a proxy measure of energy stores in the form of fat deposition, or perhaps storage of a scarce resource, such as the protein required to develop the musculature required for flight. If such a representation reflects reality, small differences in the rate of accumulation of such stores can potentially have a cumulative effect on individuals throughout the course of the spring, with knock-on effects from each of the resource 'hurdles' encountered.

The accumulation of stored mass is relatively slow in winter, but failure to reach high enough thresholds by departure from wintering areas leaves insufficient opportunity to recoup stores in Iceland. Hence, differences in individual quality (in terms of ability to acquire such reserves at critical periods) can affect the amount of mass accumulated and the amount available for investment in migration and ultimately reproduction.

This model is useful when compared with actual data compiled in the previous chapters. If the cost of egg production in Greenland White-fronted Geese is calculated using the methods of Meijer & Drent (1999), it is possible to estimate the mass required to produce a clutch of 3 or 6 eggs and then to incubate these (Table 9.1). Using the field estimates of abdominal profiles as a crude index of body mass throughout the period, it is possible to construct a graph of changes in mass of adult male and female geese up to the point of laying. The investment by the female in clutch production and incubation can then be assessed relative to the body mass available at the point of first egg production (Figure 9.2). From this, it can be seen that the costs of laying a clutch of 6 eggs takes the 'median' level of female body mass well below the lowest weights recorded throughout the annual cycle. This level is presumably well below lean body mass and hence represents starvation levels, even before the costs of incubation are considered. Although costs of self-maintenance during incubation are offset by feeding

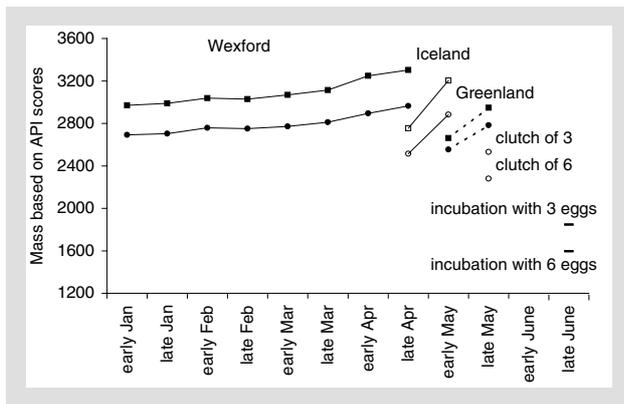


Figure 9.2. Estimated fortnightly median body mass of adult male (■ or □) and adult female (● or ○) based on field observations of abdominal profiles and their observed changes through the first half of the year. Graph contrasts the slow accumulation of stores at Wexford (solid symbols, solid line) with the rapid accumulation in Iceland (open symbols solid line) and in Greenland (solid symbols dotted line). Costs of laying 3 and 6 egg clutches have been subtracted from the late May median values, and costs of incubation from these values (based on fat and protein costs from Table 9.1). Note that this approach underestimates body mass at all stages because of the effects of using fortnightly means, hence the differences in some measures compared to direct mass determinations used earlier.

during recesses from the nest by the female, these bouts are rare and of short duration (see chapter 6). It would therefore seem that, based on observations of the 'median' female and the calculations presented here, meeting the energetic and nutritional costs of laying a clutch and completing successful incubation is not possible. On this basis, most females in any given year are unlikely to attain nutrient and energy thresholds necessary to reproduce. That said, observations from several years indicate considerable individual variation in abdominal profiles between individuals. Indeed, some birds show considerably faster rates of accumulation of body mass than do others. It seems likely, therefore, that only those relatively few individuals able to accumulate stores at rates well above the mean throughout the prelude to breeding will therefore have the potential to attempt to breed. On this basis, it would appear that a large proportion of geese could potentially arrive in west Greenland having failed to reach threshold condition for successful reproduction.

The crucial questions, therefore, concern the mechanisms that are likely to affect the ability of the individual to acquire the necessary nutrients

for survival and reproduction at each critical stage. Assuming that the environment is not unlimited in its ability to supply nutrients, a critical factor is likely to be the local density of geese. This factor affects the ability of an individual to achieve threshold nutrient requirements. What factors enable some individuals to survive and breed whilst others cannot? There is abundant evidence that amongst relatively long lived avian species such as geese, breeding performance increases with age (e.g. Owen 1984, Forslund & Larsson 1992, Cooke et al. 1995). More older birds attempt to breed than among young age classes and a greater proportion of older birds breed more successfully. For example, Raveling (1981) found although geese 4+ years of age comprised 26% of the potential breeding population, they produced more than 50% of young in Giant Canada Geese *Branta canadensis maxima*. Specifically, older birds lay earlier, larger and heavier clutches than young birds, which ultimately result in more offspring fledged.

However, reproductive performance in geese generally increases only for the first 5-6 years of life (Rockwell et al. 1983, 1993, Forslund & Larsson 1992). This is not consistent with the hypothesis of reproductive restraint in younger years (Curio 1983), which would predict increasing reproductive effort throughout life. It would therefore appear that in many goose populations, young individuals are constrained from performing well, perhaps through the lack of social status that permits access to best feeding opportunities.

Dominance hierarchies have long been recognised in goose flocks (Boyd 1953, Hanson 1953, Raveling 1970) and rank has been shown to increase with age (Lamprecht 1986, Black & Owen 1995). However, amongst birds of the same age class, dominance explained much of the variation in reproductive performance, suggesting this was the overriding factor (Lamprecht 1986, Warren 1994). Most evidently, dominance determines individual feeding opportunity through securing and defence of best feeding opportunities (e.g. Teunissen et al. 1985, Prop & Loonen 1988, Prop & Deerenberg 1991, Black et al. 1992). This in turn has consequences for food intake rates, since peck rates and feeding rates have been found to correlate positively with dominance (e.g. Warren 1994). Social status also affects whether a goose pair is able to obtain and hold a nesting territory. In situations where predation limits output, hatching success and fledging rate were also correlated

with rank. This suggests that dominant pairs were better at securing the best nest sites, as well as protecting eggs and broods from predation (Warren 1994).

The establishment of such dominance hierarchies clearly offers a mechanism that results in asymmetric patterns of individual nutrient acquisition in a situation where resources are limiting. Young, inexperienced birds (or those of poor quality) have low social status relative to older (or better quality) individuals. They therefore lack both access to nutrients and the skills necessary to maximise food intake rates, and suffer reduced fitness as a result. Indeed, recent evidence suggests that low reproductive success in early years is due to the inexperience of paired females in food and feeding area selection. This specifically hinders their ability to build up reserves in preparation for nesting (Black & Owen 1995). In that study of Barnacle Geese, declines in reproductive success in later years were attributed to the male, and thought to be linked to declining fighting ability, which determines access to optimal feeding sites for the female and acquisition and defence of best nest sites (Black & Owen 1995). Hence, within a pair, the ability of both individuals to maintain social and nutrient status (of different nature) has an impact upon their reproductive success at different times throughout the duration of the pair bond.

In its recent evolutionary history, the Greenland White-fronted Goose was a specialist feeder. It exploited the highly nutrient rich overwintering organs of a very narrow range of species associated with a rare and localised biotope (*Sphagnum*-filled depressions) in a geographically restricted habitat type (oceanic pattern mire systems restricted to the western fringe of Europe, **chapter 2**). The use of such a resource also necessitates an appreciation of the periodic recovery patterns of such a finite food source over more than one growth season. This might favour a process of cultural learning to effectively exploit patchy feeding resources in time (e.g. sequential exploitation cycles of *Phleum* over a few days and of *Eriophorum angustifolium* over at least 2 years) and space. Seen in this historical context, a long-lived herbivorous goose species with such a highly specific diet would be subject to severe limitations on resource availability. This is especially the case on the 'survival' habitat where the fitness consequences of food availability are potentially likely to affect mortality as well as reproductive output. Selection seems highly likely to favour indi-

viduals that can maintain extended family links. These enable the youngest (and potentially the most socially inferior) birds to retain high social rank by continued association with their parents, siblings and other kin (i.e. groups with the highest social status). In this way, youngest birds can elevate their functional social rank and, by association with near kin in large groups, can gain access to (and defend) best feeding patches. At the same time they gain experience and competence in feeding skills, knowledge of migration routes and staging areas and even observe and/or assist in breeding attempts by their parents on the nesting areas (MS11, MS12). Other group members benefit from the association through shared vigilance and food finding, and the parents benefit by shared vigilance in pre-nesting feeding and in nest defence on the breeding areas. In a relatively long-lived bird, the gain in social status and learned experience during the younger years might offset the loss of breeding potential in this period, which represents an investment in future breeding potential when departure from the family unit finally takes place.

Given that reproductive success first increases and then declines in later years within all studied goose populations (see above), this long association with kin ultimately bears a cost in forgone reproductive output. Ultimately, the balance of the conflict between the cost of remaining with kin versus lost reproductive output should tip towards investment in the individual's own reproduction rather than that of kin. Only in the case of poor quality individuals is it likely that the benefit of helping in the reproductive success of related birds outweighs that of pairing and leaving the family to invest in its own reproductive future. Hence, at some point, a young bird must pair up, leave the family group and effectively lose social rank and fall to the level of a 'flock of two' in the population as whole. This mechanism, whereby potentially the most fit, fecund animals must temporarily lose social status by sacrificing their links with the dominant groups in an attempt to breed, is apparently unusual amongst geese. Family break-up occurs most frequently during the first or second winters amongst studied goose species. Nevertheless, in a resource-limited system, this offers a density-dependent regulatory mechanism for recruitment of Greenland White-fronted Geese into the breeding population.

It is not possible to know whether the prevailing

social system has traditionally regulated recruitment into the reproductive classes in the Greenland White-fronted Goose population, but it is tempting to speculate this was and remains the case. The population is characterised by unusually prolonged parent-offspring relationships (25% were still associated with one parent in their seventh winters, MS 11), even compared to other races of White-fronted Geese (Ely 1993). Yet the production of young per successfully breeding female (measured by family brood size on the wintering grounds) is unusually high compared to most other goose populations, consistent with the idea that only the highest quality pairs breed in any one year. These features are consistent with a social system that enables successful pairs to maintain high social status through persistent association of earlier offspring, which seem likely to remain with their extended families because of the high relative cost of pairing and losing such status. Reproduction in the population as a whole therefore involves a relatively low proportion of the potentially reproductively active individuals - generally only those of high quality (see Figure 9.1 and 9.2 above).

Under legislative protection from shooting on the winter quarters, the population has shown an increase consistent with constant adult survival and observed breeding success rates. If some density dependent function were involved, whereby the overall number of opportunities to nest in any one year were limited to the same number every year, it might be expected that, above this threshold level, entry into the breeding class would be severely limited. There is now some emerging evidence to suggest that such a limit exists for the Greenland White-fronted Goose. Amongst those wintering at Wexford and Islay (some 60% of the total population), the number of successfully breeding pairs returning with young steadily increased during the 1970s, although production in any one year varied with summer temperature in Greenland (Figure 9.3). Since protection from hunting, the absolute number of successful breeders has been stable at c.1,000 pairs in years when cold summer conditions have not limited successful breeding (Figure 9.3). There does seem therefore to be a current limit to the number of pairs that can breed successfully amongst birds using these two wintering resorts (**chapter 6**). This is manifest amongst the marked population in falling recruitment levels amongst cohorts hatched since 1984, partly a result of delayed age of first breeding amongst this sample

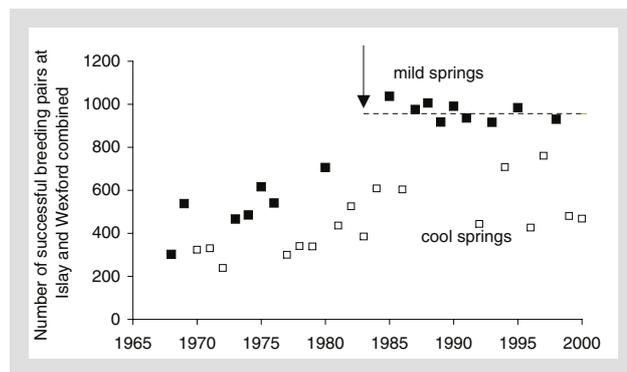


Figure 9.3. Total number of successfully breeding pairs (i.e. parents returning with at least one young) in autumn from Islay and Wexford combined. Open symbols are years with cooler than average June temperature in West Greenland, solid symbols warmer than average (based on data from Zöckler & Lysenko (2000)). Note the apparent constant maximum number of successful breeding pairs since protection (arrow) in seasons of above average summers.

but also declining brood size amongst those that breed (**chapter 6**).

The demographic data support the idea that there is an apparent current 'ceiling' to reproductive output in this population, but it is far from clear how this limitation is exercised. There might be a limit to the extent of breeding habitat or number of nest sites, but these seem highly unlikely, given the wide extent of available habitat (**chapter 6**). Furthermore, the limit could be to brood rearing nursery habitat, or to the post fledging survival of young. Both of these factors also seem highly unlikely, given that a density dependent mechanism would tend to reduce brood size (for example, as a result of losses of smallest goslings Owen & Black 1989), rather than result in a loss of entire broods from the population. In the Greenland Whitefront, a characteristically low proportion of successful breeders return with unusually large families compared to other geese populations.

Hence, it would therefore appear that relatively few pairs attempt to breed in any one year, and amongst those pairs which do, the majority breed successfully, in terms of raising large numbers of young per family that survive to reach the wintering grounds. As discussed above, this could be the result of density-dependent limitation in access to nutrient acquisition on the wintering grounds, the Iceland spring staging areas, in Greenland during pre-nesting feeding or a combination of all three. Since the extended family relationships persist on the wintering, spring stag-

ing and (to a lesser known extent) pre-breeding areas, it seems likely that a brood female with attendant offspring from previous years obtains considerable advantages for nutrient acquisition during all three phases of the prelude to breeding. Furthermore, the association of offspring from previous years could potentially enhance nest defence and protection of subsequent hatched young. In contrast, lone pairs face considerable disadvantages owing to their low social status, which denies them access to the best feeding opportunities. They must increase food intake rates to compensate for loss of access to richest food patches by consuming higher quantities of lower quality foods to meet threshold levels of stores needed to attempt reproduction. Even after laying a clutch, the lone pair lacks kin associates for nest defence from predators.

It therefore seems most likely that there is a limit to individuals entering the breeding class and this limitation is likely to be condition based. It is already known that pre-nesting feeding areas are spatially limited in spring and patterns of snow-melt could impose further limits on food availability (see Glahder 1999). Hence, pre-nesting spring food availability is likely to specifically limit resources available to potential brood females. Only those individuals most efficient at nutrient accumulation in the period up to and immediately after arrival in Greenland can achieve the necessary stores for successful reproduction.

9.2 The impact of hunting mortality

In the absence of histories of individually marked birds from the years when hunting occurred in all seasons, it is impossible to determine the true effects of winter hunting mortality on Greenland White-fronted Geese. The comparison between Haldane estimates of survival before and after protection suggests hunting was additive. The simple modelling exercise included here (**chapter 8**) gives some support to the hypothesis that completely additive hunting mortality at Wexford would explain the period of stable numbers during 1969-1982, and the observed rate of increase after protection. However, in the two years when hunting was permitted on the Wexford Slobs since 1982, there was no convincing difference in annual adult or juvenile survival based on resightings of individually marked birds.

However, the unusually high mortality in one

year (1989) which resulted in 75% mortality amongst young and reduced adult survival demonstrates the sensitivity of the population to such occasional stochastic events, and their impact on subsequent population trends. As previously demonstrated, the population is highly sensitive to small changes in annual adult survival rates (Pettifor et al. 1999), and therefore, it is not surprising that the removal of winter hunting had an immediate effect on population trajectory. Given this direct impact of changes in survival rate on change in population size, it does appear that protection from hunting was the cause of the increase in numbers in the population after 1982. The site-safeguard programmes of the last 20 years have only contributed in so far as protection of regularly used roost sites and other protected areas have guaranteed their perpetuation.

An interesting feature of the relationship shown in Figure 9.3 is the apparent 'jump' in the number of successful pairs which returned to Islay and Wexford in warm summers following protection from hunting on the wintering grounds. There seem some grounds for believing that the levels of recruitment amongst these wintering elements of the population increased rapidly to the current (apparently limited) level immediately following cessation of hunting. In the absence of resighting histories of individually marked birds before and after protection, it is impossible to explain this phenomenon in terms of individual behaviour. Nevertheless, it is interesting to speculate as to whether hunting has an effect on reproductive success in the population as well as a direct effect on adult annual survival. Such a relationship could be the result of the effects of wildfowling disturbance to geese, known to affect breeding success in some populations (Madsen 1995). However, it is also clear from observations on the wintering grounds that extended families tend to fly in small unattached groups, whilst non-breeding elements of the population aggregate into large flocks (unpublished data). Hence, although families form a very small proportion of the overall population, their potential frequency of encounter by a hunter is disproportionately high. Observations of behaviour of wildfowling Pink-footed Geese in west Jutland, Denmark have shown that hunters tend to shoot at individual goose flocks as these are encountered. In that study, family groups were more likely to be shot at than large flocks of geese not because of their numerical abundance, but simply because of their greater frequency of encounter with hunt-

ers (J. Madsen unpubl. data). In this way, wildfowling could potentially select for the experienced breeding adult element of the population, even though these individuals are numerically few amongst Greenland White-fronted Geese. Hence, through the death, or sub-lethal crippling of one or both partners of an experienced pair, the most productive element of the potentially breeding population is being lost by break up or total loss of successfully breeding pairs. Although there are no data to support such an assertion, this would provide some explanation for the secondary effect of the cessation of winter hunting on the increased reproductive output of the population since the early 1980s. It would be essential, should winter hunting ever be reinstated in this population, to at least monitor these secondary effects on the population dynamics of the race, in addition to tracking the direct effects on annual survival rates.

At present, we can say little about the effects of the continuing kill of some 3,000 birds in Iceland on autumn migration every year, but it is clear that removal of this number of birds has not stopped the increase in the population over the last 25 years.

9.3 Current conservation issues of concern

It would therefore seem that the population was restored to favourable conservation status by simple legislative manipulation of human-induced mortality processes. Restrictions on hunting have undoubtedly restored this population to a more favourable conservation status since 1982, most notably at Wexford and Islay, where a direct effect can be demonstrated. However, amongst the numbers wintering elsewhere in Britain, flocks continue to decline and disappear. Having reversed the overall decline in the population, the next priority is to identify factors affecting the continuing declines and extinctions that are occurring at wintering areas other than the major sites. This is necessary in order to achieve the declared aim of maintaining the current geographical range of the population.

A variety of land-use changes have been taking place since the early 1980s in Britain and Ireland. In the 1980s and 1990s, intensification of grassland management (especially on Islay) resulted in many birds wintering there moving to feed on

new rotational grass leys. This might have resulted in geese retaining higher levels of nutrient and energy stores throughout the winter period than would have been possible on more traditional natural and semi-natural habitats. This in turn brought Greenland White-fronted Geese into local conflict with agriculture (including shooting mortality permitted under licence). Now, with the cessation of dairying on Islay in 2000, there is the prospect of wide scale changes in grassland management on that island, this time involving reduction in levels of management intensity in some areas. In addition, many of the outlying flocks in Scotland and Ireland were affected by the general decline in the rural economy, with the result that low intensity agricultural land has become abandoned or neglected in recent years. Hence, away from the large concentrations, geese are facing habitat loss and degradation.

Even at Wexford Slobs, there have been substantial changes in land use in the last 50 years. This was initially through improvements to grassland management techniques, but in the last two decades due to increasing tillage (including cultivation of crops such as carrots, maize and linseed) and even forestry on the South Slob (now largely lost as a goose feeding resort in very recent years). Hence, the geese have faced a range of different changes to land use at wintering resorts over differing time scales. Can we learn anything from the historical perspective regarding goose responses to changes in agricultural practice? Given the competition from Canada Geese and/or global climate change look set to affect the population adversely through impacts on the breeding grounds, what mitigation measures on the wintering areas might be possible or appropriate to reverse these trends?

There is considerable evidence to suggest that the flocks declining most rapidly are those with the fewest and least extensive feeding areas (MS14). Although a link has never been demonstrated, it seems likely that these sites are the most susceptible to disturbance by humans, since their restricted winter range limits escape options to undisturbed areas (Norriss & Wilson 1988). It is important to determine for those flocks whether the changes in number are due to changes in demography (i.e. low survival and/or fecundity) or patterns of immigration and emigration. Although there have been many studies of the effects of disturbance on birds (e.g. affecting spatial distribution, Madsen & Fox 1995, Fox &

Madsen 1997, Madsen 1998), demonstrating impacts at the population level have proved more difficult (Madsen 1995). If it is possible to establish such links, it becomes more possible to address the causal factors, identify the points in the life cycle at which these factors operate and implement management to mitigate such factors. Does poor feeding opportunities and/or disturbance directly affect survival or breeding success, and what are the proximate causes? It is well demonstrated that disruption to feeding patterns on spring staging areas prior to migration to breeding areas affects the reproductive potential of geese (Madsen 1995), but what of disturbance at other times of year?

Given the relative slow build up in body stores throughout the winter in this population, it may seem less likely that disturbance in mid-winter could affect departure condition than during the spring pre-departure phase. In comparing between individuals, Figure 9.1 shows graphically how reduced rates of mass accumulation could result in longer term fitness consequences, but such a model could equally apply between sites. Where nutrient and energy acquisition is reduced relative to best feeding opportunities, the potential to attain store thresholds at staging areas later in the annual cycle is diminished. Birds departing from poor quality or highly disturbed wintering areas may not be able to compensate in Iceland and Greenland, and hence may suffer reduced fitness as a consequence. Indeed, if the numbers of geese wintering on high quality habitats increases, and these birds depart in good condition, birds departing in poor condition from wintering areas are likely to face even greater competition in spring if food resources in Iceland and Greenland are limited. Hence, a mechanism of intra-specific competition operating away from the wintering areas may actually be influencing the relative changes in abundance of Greenland White-fronted Geese at different wintering resorts.

Climate change may play a role at several stages in the life cycle of the geese. There is a trend amongst Greenland White-fronted Geese for the most southern wintering flocks to show the most dramatic declines (MS14). The recent declines at Wexford are attributable to falling fecundity at that site at least, but does this hold for other wintering flocks in the south of Ireland showing similar trends? Is this reduction in breeding because of global climate change affecting their breeding conditions in the north of their west Greenland

range? Or could it be that the same climate change is affecting the phenology of growth of food plants exploited in spring on the wintering areas and staging grounds in Iceland? Could the spring flush of grass production in southern Ireland (the so-called "spring bite") be occurring earlier and earlier as a result of climate change, that it occurs too soon for geese to effectively exploit? A full exploration of the weather archive needs to be undertaken before we can answer such questions. Furthermore, the patterns of change in goose numbers at different wintering resorts need to be investigated in terms of their demography and distribution, before it is possible to identify what environmental factors are likely to shape these processes.

In many areas of the summering grounds, White-fronted Geese follow the phenology of thaw in the west Greenland landscape. This involves the exploitation of plants in the early stages of growth as they are released from dormancy by the thaw, but before the onset of rapid growth. On a macro scale, this involves a movement up-hill following the general amelioration of temperature as the spring and summer progress. Later in the season, at high altitudes, this pattern reflects aspect and topography, with the geese essentially following the disappearance of late lying snow patches, which offer the last burst of plant production in the landscape. The geese especially exploit this phenology of plant growth during the moult, when their ability to switch between habitats is severely limited by their association with water bodies to which they resort when threatened by predators. The proximity of late snow patches in association with open water therefore limits available moult habitat in many areas and the timing of melt of these areas may be critical to the regrowth of flight feathers at this time. Changes to patterns of melt and hence the phenology of plant growth at different altitudes could therefore have consequences for the feeding efficiency of geese throughout the summer.

And what of the effects of competition from Canada Geese on the summering areas? Accumulating evidence suggests exclusion of White-fronted Geese from formerly occupied moult sites. If maintained, this represents net Whitefront habitat loss. If available moulting habitat is in any way limited, this will ultimately have some effect on the population as a whole, as long as the numbers of Canada Geese continue to increase. This represents yet another dimension to population

limitation which operates during another stage of the life cycle, until now relatively little studied.

9.4 Overview and future research

The freedom to fly gives long distance migratory birds the opportunity to exploit distant nutrient and energy sources in the course of their annual cycle. In particular, given endogenous sources of energy to sustain periods of flight, it enables organisms to move between islands of abundant food resources across large expanses of wholly unsuitable habitat. At the same time, this very mobility creates patterns of energy and nutrient demands in the form of expensive migratory costs, met from storage accumulated during times of resource abundance. The synthesis presented here is helpful in conceptualising the annual cycle of the Greenland White-fronted Goose as a sequence of discrete periods according to energy/nutrient acquisition or demand. Typically, this relates to periods of storage of energy and/or nutrients followed by short bursts of use of accu-

mulated stores (generally breeding events or migration episodes). However, there are also periods in the life cycle where extra demands (such as wing moult, or defence of body condition in early to mid-winter) can be met by exogenous supply (Figure 9.4).

It has frequently been asserted that evolution has minimised the overlap of energy- and nutrient-demanding periods of the life cycle of birds (the "staggered costs" hypothesis coined by Lovvorn & Barzen 1988). In the Greenland White-fronted Goose, this separation in time and space offers the possibility to specifically identify critical periods in the annual cycle. In this way, it is possible to assess the ability of individuals to reach critical condition thresholds in order to meet each of the specific demands they face in discrete periods within the annual cycle.

From the nature conservation and research standpoint, such an opportunity is fortunate in offering a framework by which to concentrate future study efforts. For each period of accumulation of

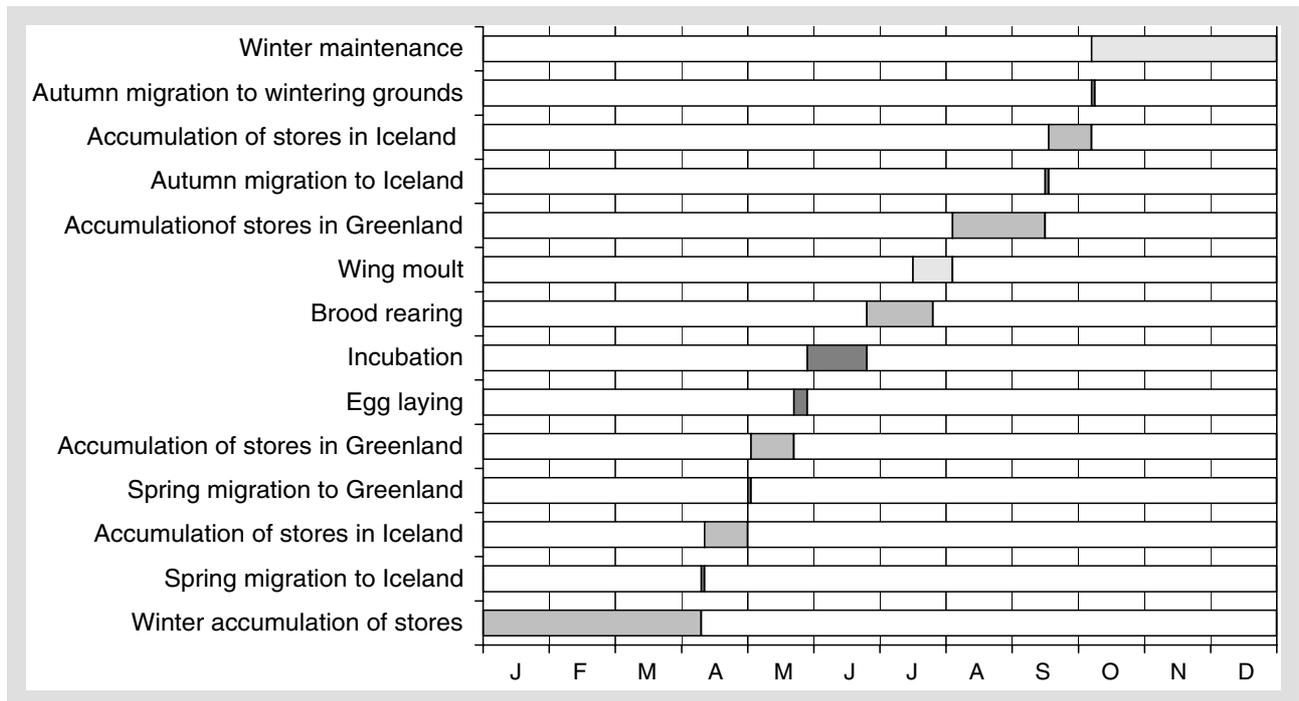


Figure 9.4. The annual cycle of an adult breeding female Greenland White-fronted Goose represented as a sequence of discrete calendar events, categorised as a series of periods of energy/nutrient acquisition or demand. These generally fall into three categories: (i) Periods of storage of energy and/or nutrients (shown cross-hatched in the bars above). (ii) Use of accumulated stores (generally breeding events or migration episodes, shown as dark bars). (iii) Periods in the life cycle where extra demands can apparently be met by exogenous supply (such as during wing moult, brood rearing or the defence of body condition in early to mid-winter, shown as shaded bars). Note that the period of brood rearing also represents a critical period for the female, during which she must recoup depleted stores and potentially reserves utilised during brood laying and incubation.

stores, the rate of acquisition (and hence condition state by a given time) will be affected by a range of factors acting on the individual. For instance, on the wintering grounds, the level to which an individual can maintain suitable food intake rates in relation to maintenance expenditure is affected by primary external factors (such as food quality or abundance). This is then modified by secondary factors (such as rates of disruption to feeding patterns through human disturbance or intra-specific interference). If we assume that the foraging ability of an individual is related to its ability to accumulate stores in anticipation of energetic expenditure, in the short term we can use measures of feeding efficiency and/or rates of change in individual condition to contrast the relative costs and benefits of differing foraging situations. Such a comparative approach based on detailed observations of marked individuals offers the opportunity to contrast, for instance, the ability of individuals of different status to accumulate stores in the presence/absence of disturbance (Madsen 1995). It becomes possible to compare rates of change in body condition based on feeding on different habitat types, or examine differences in birds of different social rank. Viewed over longer time scales, the short term ability to maximise efficiency in store accumulation ensures not only the survival of the individual but ultimately the recruitment and lifetime reproductive output of the individual. Based on the accumulated life histories of individuals, we can contrast differences in lifetime reproductive output as a fitness measure of the different strategies used by individuals throughout their lives.

On-going studies have already demonstrated the ability to detect differences in energy accumulation rates between Greenland White-fronted Geese using different grass swards during spring staging at the same site in Iceland (Nyegaard et al. 2001). From observations of collared individuals, it is known that different individuals exploit different sward types, many showing consistent patterns between years (**chapter 4**). This (not unexpectedly) appears to influence the rate of change in abdominal profile scores of individual geese exploiting different sward types (MS18 and unpublished data). The accumulation of more individual life histories with details of habitat use, patterns of store acquisition and condition on departure from Iceland will enable the assessment of the fitness consequences from such foraging behaviour in the fullness of time. These linkages

between different elements in the life cycle are essential if we are to obtain a deeper understanding of how individuals perform in terms of survival and reproduction measures with regard to the environment they exploit.

There are thus 3 measures available to assess individual performance: the balance of food intake rate versus use over short periods, the rate of accumulation of stores for completion of demanding episodes in the life cycle and ultimately the survival and reproductive output of the individual. It is possible to combine specific detailed investigation of these elements with the longer term historical resighting data, which provide records of how an individual has performed throughout its life. For geese ringed as goslings in their first winter, these records include which areas and habitats they exploited at different times of the year, when they separated from parents, how often a bird has changed wintering site, how often it returned to wintering areas with young and how long it lived. What is interesting is to see how individual decision-making can affect feeding efficiency, condition and, ultimately, fitness. Although Greenland White-fronted Geese are highly site loyal, birds do change wintering sites (MS9). In **chapter 4**, we saw how individual birds tend to specialise on a particular grass sward during staging in Iceland in spring, but some birds do show the ability to change from less nutritious swards to more profitable ones (Figure 4.9). Hence, individual decision-making enables modifications to feeding efficiency, condition and fitness, and it is the consequences of these decisions which offer insight into how individuals behave and how this contributes to overall population behaviour (Figure 9.5). Combinations of historical data and new investigations enable use of these measures to assess factors affecting individual breeding success and survival and an attempt is made to set out the major research objectives in Appendix 2.

The priorities for the immediate future are to continue to monitor the patterns in numbers and distribution which is only possible on the wintering areas (see Appendix 2 for details). The individual marking programme at Wexford must continue if we are to be in a position to interpret the changes in numbers based upon the count information. This programme should be extended to more individual marking and monitoring at other sites to construct the basis for comparative studies discussed in greater depth below. The basic ration-

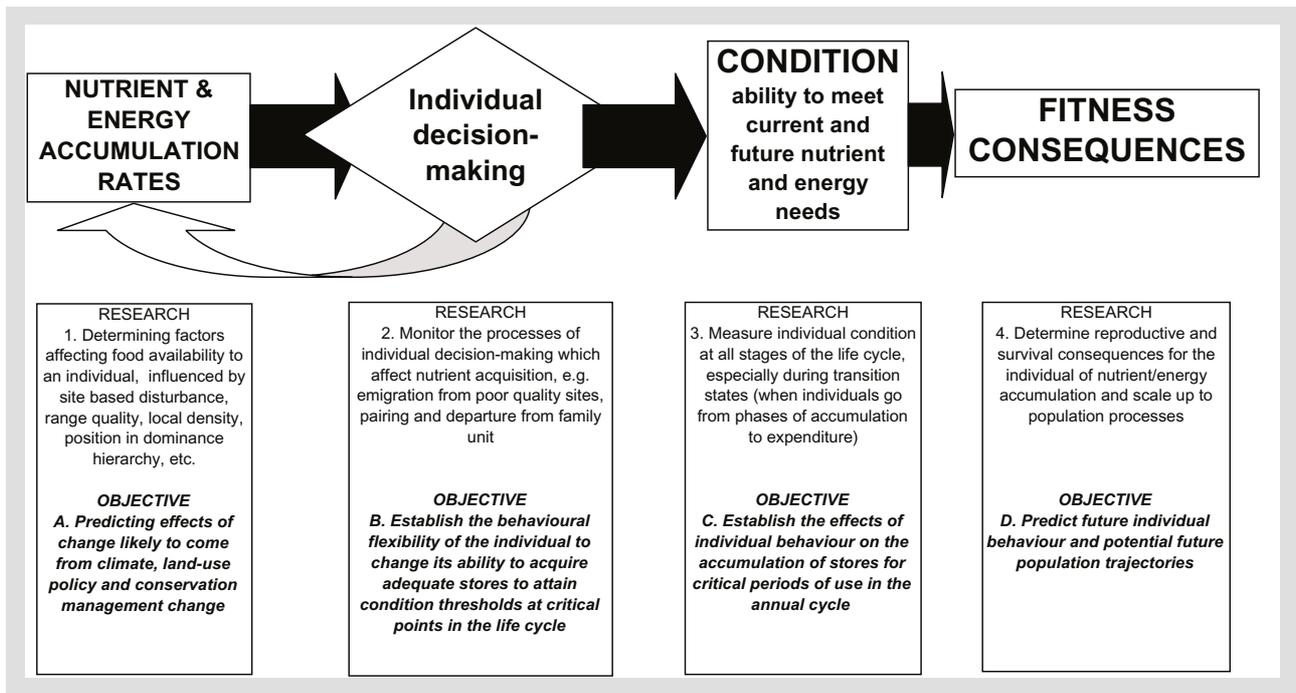


Figure 9.5. Schematic representation of the effects of nutrient accumulation rates (mediated by individual behaviour) on body condition and fitness in Greenland White-fronted Geese, showing associated research questions and objectives associated with each level.

ale for all research to date has been driven by nature conservation objectives, and although there are many curiosity driven research objectives that could be included as well, the key conservation questions are as follows: (i) What factors affect changes in abundance at wintering sites? (ii) What factors limit successful recruitment into the breeding class? (iii) How will the effects of predicted global climate change affect the population (iv) How will the Canada Goose population of West Greenland affect the White-fronted Goose population?

Armed with a means of measuring condition, it becomes possible to reformulate these questions in the context of the direct effects of food quality and factors affecting feeding rates (as a result of climate change, inter- or intra-specific competition or human disturbance). Such an approach can offer conservation management solutions on the wintering grounds (for example where intervention management can improve food quality or restriction on human activity can reduce disturbance to feeding patterns). Using measures of condition on the pre-breeding spring staging areas, it becomes possible to measure and contrast density-dependent effects amongst potentially breeding females in the prelude to clutch initiation and investigate the role of nutrient limitation and effects of competition at this time.

Such empirical relationships are vital for our understanding of small-scale population processes and individual behaviours. However, there remains a need to generate large-scale predictions about the effects of, for instance, macro changes in land use on the wintering grounds, or the effects of climate change throughout the entire geographical range. From the point of view of contributing to predictive models, such investigations also provide basic data regarding the behaviour of individuals in response to local goose densities or their position in dominance hierarchies. When does a goose of potential breeding age pair and how is this decision condition mediated? What conditions make an established pair emigrate from a poor quality winter site to another site? What are the fitness consequences of changing site for low, medium or high ranking birds at wintering sites of different quality?

Perhaps most important, the measure of the capacity of individuals to make adjustments to their annual cycle which potentially improve fitness measures gives the potential to assess the flexibility of the population and its capacity to exploit novel opportunities. This element is important. In the past, it has been difficult to predict the patterns of development in the abundance of wild goose populations. From the low levels of abundance in the 1930s, protection measures put

in place from the late 1940s onwards in the United Kingdom ensured the increase in goose numbers to the present day. However, the numbers of several populations stabilised in the 1970s and 1980s, generally thought associated with density dependence (e.g. Figure 1 in Pettifor et al. 2000). Largely unseen from the perspective of the wintering grounds, Pink-footed Geese nesting in Iceland and Barnacle Geese in Svalbard expanded to new colonies, and showed renewed periods of increase that could not be predicted on the basis of population-based models constructed using demographic data from previous years.

It is often extremely difficult to determine the strengths of density dependence in empirical studies (e.g. Pollard et al. 1987). Historical population data are likely to be collected over a very narrow range of population sizes and environmental conditions, unlikely to offer the basis for robust predictions for the future (see discussion in Pettifor et al. 2000). For this reason, it has been argued that models predicting the response of a population to environmental change need to be based upon the aggregative total of individual behaviours (Goss-Custard 1985, Goss-Custard & Durell 1990). In this way, models can be developed to predict effects of change in the environment on a population based on the cumulative sum of individual responses under novel circumstances. Such models have been developed using game theory to explore how individuals of varying competitive ability can exploit a patchy and variable food supply. The classic models have been built based upon maximising individual fitness in Oystercatcher populations, by Goss-Custard and co-workers at individual site (Goss-Custard et al. 1995a,b) and at population levels (Goss-Custard et al. 1995c,d). Such models need to be large scale and encompass the entire annual cycle, as exemplified by the application of Pettifor *et al* (2000) to other goose populations. The application of such models to the Greenland White-fronted Goose would identify the key model parameters required and could prove extremely important to our understanding of future potential change.

9.4 Conclusions

There is accumulating evidence to suggest that during the latter half of the 19th Century, the Greenland White-fronted Goose began a shift in habitat use from very limited small-scale habitat

types to emerging (and far less geographically restricted) agricultural habitats. Nevertheless, the population has continued to be geographically restricted by virtue of its winter site fidelity, and continues to probe for the underground storage parts of plants (bulbils, stolons, rhizomes, etc.), even in current agricultural landscapes, far more than other western European goose populations. Greenland White-fronted Geese appear behaviourally constrained by inherent site fidelity and a general conservatism with respect to the exploitation of novel habitats. Only one small new wintering flock is known to have become established in the last 25 years (MS14). Although geese have shown shifts from natural and semi-natural feeding habitats to managed grasslands, these have only occurred when these grasslands are created in close proximity to existing feeding areas. While there are abundant areas of such grasslands available throughout Scotland and Ireland, currently unexploited by Greenland White-fronted Geese, there are no signs of colonisation of such suitable habitat away from traditionally used roost sites. Hence while the potential for extensive spread of the population looks possible, the capacity of the population to do so has been limited to in-filling in close proximity to existing home ranges exploited by the current wintering flocks.

Assuming that this site fidelity holds for other periods of the life cycle, its potential breeding, staging and wintering range is geographically limited. This inevitably limits the potential carrying capacity of the habitat globally and is likely, at some stage, to lead to an eventual limitation on total population size. Nevertheless, as we have seen, different habitats have the potential to limit population change in different ways, and to return to the ideas of Alerstam and Högstedt, these can be divided into 'breeding' and 'survival' habitats, where such factors may operate. Hence, we can conceive of winter, spring staging and pre-breeding habitats as comprising the 'breeding' habitat in so far as any or all could potentially limit reproductive output in the population as a whole. Equally, we could conceive of 'survival' habitat including the moulting areas in Greenland, since the successful regrowth of flight feathers is essential for flight, to enable movement between all the geographical areas used by geese in their completion of the annual cycle.

Hence, breeding and survival habitats and the life cycle processes completed in these habitats are not necessarily limited to breeding and non-

breeding geographical locations respectively. Critical elements in the annual cycle can occur at different places in time and space, and accordingly factors that regulate the rate of change or limit population size can affect population dynamics in different places at different times. In the case of the Greenland White-fronted Goose, we begin to see that different mechanisms have limited the size of the population in the very recent past. This has either been through the maintenance of low (relative to potential) annual survival rates through hunting on the wintering grounds, or through recent declines in fecundity due to apparent restrictions of entry to breeding age class (potentially through restrictions on pre-breeding condition of females). Hence, we have seen a population that was maintained at a level below its potential by hunting kill expand in response to protection from winter hunting. The present rate of population increase shows signs of slowing in the last few years, despite no decrease in annual adult survival, showing that some other mechanism is responsible. This is due to falling fecundity, with a stable number of breeding pairs returning to wintering grounds with young despite increasing population size. At one wintering site, Wexford, this trend has ultimately resulted in a decline in wintering numbers. This may to some extent be the result of a run of summers with low June temperatures. This may in turn be a consequence of global climate change that has made, and is predicted to continue to make, summers in northern west Greenland cooler in coming years. Hence this trend may become manifest elsewhere if patterns of climate change continue as predicted.

The conservation message from this type of study is clear. We need to be able to understand the role of different processes throughout the annual cycle of such populations and we need to be able to monitor these processes and their effects. It is important to be able to establish which factors affect a population in which ways and at which periods in the annual life cycle. It is not enough to establish patterns in survival and reproduction at one wintering site and expect to be able to understand the processes that shape the changes in total numbers from year to year. Although it is possible to make some inferences about the patterns of population change, as is evident here, it is not yet possible to demonstrate causal relationships. Conservation needs more examples of experimental manipulation of legislation and their demographic repercussions on population change,

in order to be more confident in predicting the effects of change. In fact, there exist very few good examples of this (see Nelson & Bartonek 1990). In North America, the implementation of adaptive waterfowl management strategies ('wildlife management by experimentation', MacNab 1983) has met with mixed success (Johnson & Williams 1999). One major problem with, for example, attaining the objective of determining the effects of hunting harvest on annual survival has been the conflict between maximising the hunt harvest and maximising the knowledge derived from experimental manipulation of the hunting bag. Nevertheless, it is essential to understand the strength of such processes, including, for example, the strength of density dependence and the extent to which differences in individual behaviour determines the access of individuals to necessary nutrients. It is also necessary to demonstrate the extent to which hunting mortality is additive. If it can be demonstrated that hunting mortality is partially compensatory, sustainable hunting can be maintained below a critical threshold without seriously reducing total population size.

All these effects require monitoring of change in numbers in the population as a whole, whether this is achieved through annual winter census (including proportions of young present to establish breeding success and, by difference, survival), or surveys of the pre-breeding, nesting or moulting areas. It is essential that at least winter inventories and measures of breeding success are maintained, as these remain the only practicable means of monitoring the numbers and breeding/survival processes in the population. Although it is difficult to maintain count coverage by observers in remote areas (where conditions may be logistically difficult), this remains the absolute priority to extend the present time series. At the moment, there are no attempts to carry out regular aerial survey of spring staging, nesting and moulting areas in Greenland, although all have been carried out on a limited basis in the past. These three periods are, as we have seen, critical ones in the annual life cycle and regular (e.g. every five years) survey of these would be highly desirable. Such information might provide great insights into the way local conditions (including local goose densities) may affect dispersal, survival and reproduction.

Nevertheless, if we are ever to be in a position to interpret the reasons behind observed changes in population changes, we must continue with the

study of the behaviour of marked individuals. We can use capture-mark-recapture programmes to estimate survival, follow reproduction, measure rates of individual emigration/immigration from wintering sites and determine individual life-time reproductive success and dispersal patterns which offer insights into how changes at the population level are manifest. Such information is vital if we are to understand the changes at population level and determine how density affects the individual, in terms of recruitment and survival probabilities, with respect to individual quality. Since populations are composed of individuals of differing quality, it is important to be able to show how competitive ability, age, experience and social status of the individual affect food intake rates, store acquisition and ultimately fitness measures. Greenland White-fronted Geese are long lived and may take six or more years to enter breeding age classes. For this reason, it is increasingly important to mark a representative sample of individuals on a regular basis over many years, to generate resightings of individuals and contribute to life histories that establish asymmetry in dispersal, fecundity and survival with regard to specific behavioural traits. In particular, it is increasingly important to maintain a pool of marked birds to form the basis for studies of differences in nutrient acquisition throughout the annual cycle. There have been no specific behavioural or energetic investigations relating to the effects of social status and age on access to best quality food patches, peck rate and general levels of nutrient and energy acquisition. The relatively large numbers of marked individuals in this population, together with their extreme site loyalty, offer exciting possibilities in this respect. It is not enough to suggest that dominance hierarchies potentially skew the ability of an individual to acquire body stores, there needs to be some direct evidence of how and why this is achieved.

The lack of detailed information relating to geese from this population wintering away from Wexford is lamentable. Given the difference in demographic patterns between Wexford and Islay, it would be highly desirable to resume a programme of regular capture-mark-recapture of individuals on Islay, preferably through a programme of collar marking in parallel to those at Wexford. Catching throughout the season at other sites would generate data on seasonality of mass

changes at other resorts for comparison with the pattern from Wexford. We need to learn more about the habitat use and other factors affecting numbers at lesser winter resorts, especially those that give immediate concern for their well being. At present, we do not know if the declines at such sites are due to poor survival, low reproductive success, high emigration, low immigration or a combination of some or all of these factors. Again, it is important to establish the causes of these changes before it is possible to tackle the conservation challenge through implementation of management action.

Finally, having identified the key elements that potentially influence survival rates and fecundity, it is essential to test these in the field to establish some level of causation. Is climate change driving the difference in reproductive output at Wexford and Islay? Both wintering aggregations are showing declines in individual female fecundity, but this is greater at Wexford, where the effect has been to cause an overall decline in numbers not attributable to increases in the balance of emigration/immigration, nor to changes in annual survival. Is this because of changes in habitat at Wexford, cooler summers on the more northerly breeding areas which Wexford birds tend to use, or a combination of these factors? We need simultaneous studies of reproductive output from different parts of the breeding grounds with respect to local meteorological conditions from a number of years to establish the trends and patterns in breeding success. This would provide a firmer platform for predictions of the effects of global climate change than is possible at present, and enable generation of population predictions for changing scenarios as global climate models improve. We also need to understand how density dependence is manifest through dominance hierarchies – what are the real costs and benefits to an individual (e.g. in terms of fat or protein accumulation rates) of being part of a large group, or situated at the bottom of the league of social status? We need to be able to quantify these relative costs and benefits before we can be in a position to understand the function of such status and the strength of its effect in terms of fitness consequences for individuals. Only by understanding the behaviour of the individual will we be in a position to predict the future behaviour of the entire population.

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12 Appended manuscripts

- 1: Fox, A.D. & Madsen, J. (1981) The pre-nesting behaviour of the Greenland White-fronted Goose. *Wildfowl* 32: 48-54.
- 2: Fox, A.D., Madsen, J. & Stroud, D.A. (1983) A review of the summer ecology of the Greenland White-fronted Goose *Anser albifrons flavirostris*. *Dansk Ornitologisk Forenings Tidsskrift* 77: 43-55.
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- 12: Fox, A.D., Boyd, H. & Bromley, R.G. (1995) Mutual benefits of associations between breeding and non-breeding White-fronted Geese *Anser albifrons*. *Ibis* 137: 151-156.
- 13: Fox, A.D., Glahder, C., Mitchell, C., Stroud, D.A., Boyd, H. & Frikke, J. (1996) North American Canada Geese (*Branta canadensis*) in West Greenland. *Auk* 113: 231-233.
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Addresses:

URL: <http://www.dmu.dk>

National Environmental Research Institute
Frederiksborgvej 399
PO Box 358
DK-4000 Roskilde
Denmark
Tel: +45 46 30 12 00
Fax: +45 46 30 11 14

Management
Personnel and Economy Secretariat
Research and Development Section
Department of Policy Analysis
Department of Atmospheric Environment
Department of Marine Ecology
Department of Environmental Chemistry and Microbiology
Department of Arctic Environment
Project Manager for Quality Management and Analyses

National Environmental Research Institute
Vejløsøvej 25
PO Box 314
DK-8600 Silkeborg
Denmark
Tel: +45 89 20 14 00
Fax: +45 89 20 14 14

Environmental Monitoring Co-ordination Section
Department of Terrestrial Ecology
Department of Freshwater Ecology
Project Manager for Surface Waters

National Environmental Research Institute
Grenåvej 12-14, Kalø
DK-8410 Rønde
Denmark
Tel: +45 89 20 17 00
Fax: +45 89 20 15 15

Department of Landscape Ecology
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