

Feeding behaviour and competitive interactions
of the Greenland White-fronted Goose
Anser albifrons flavirostris

*with special emphasis on spring staging geese in Iceland
and moulting geese in Greenland*

Ph.D. Thesis

Jens Nyeland



Department of Population Ecology

Zoological Institute

Faculty of Science

University of Copenhagen

January 2001

Feeding behaviour and competitive interactions of the
Greenland White-fronted Goose *Anser albifrons flavirostris*

with special emphasis on spring staging geese in Iceland and moulting geese in Greenland

Ph.d. thesis

Jens Nyeland

*Department of Population Ecology
Zoological Institute
Faculty of Science
University of Copenhagen*

January 2001

Cover drawings by Bill Neill

CONTENTS

1. Preface	4
2. Acknowledgements	5
3. Synopsis	
3.1 Introduction	6
3.2 Iceland	7
3.3 Greenland	14
3.4 References	18
4. Manuscripts	
1. Fox, A.D., Hilmarsson, J.Ó., Einarsson, Ó., Boyd, H., Kristiansen, J.N., Stroud, D.A., Walsh, A.J., Warren, S.M., Mitchell, C., Francis, I.S. & Nyegaard, T. 1999. Phenology and distribution of Greenland White-fronted Geese <i>Anser albifrons flavirostris</i> staging in Iceland. <i>Wildfowl</i> 50: 29-43.	
2. Fox, A.D., Hilmarsson, J.Ó., Einarsson, Ó., Walsh, A.J., Boyd, H., Kristiansen, J.N. (accepted) Staging site fidelity of Greenland White-fronted Geese in Iceland (<i>Bird Study</i>).	
3. Boyd, H., Fox, A.D., Kristiansen, J.N., Stroud, D.A., Walsh, A.J. & Warren, S.M. 1998. Changes in abdominal profiles of Greenland White-fronted Geese during spring staging in Iceland. <i>Wildfowl</i> 49: 57-71.	
4. Kristiansen, J.N., Fox, A.D., Boyd, H. & Stroud, D.A. 2000. Greenland White-fronted Geese <i>Anser albifrons flavirostris</i> benefit from feeding in mixed-species flocks. <i>Ibis</i> 142: 142-144.	
5. Kristiansen, J.N., Fox, A.D., Stroud, D.A. & Boyd, H. 1998. Dietary and microtopographical selectivity of Greenland White-fronted Geese feeding on Icelandic hayfields. <i>Ecography</i> 21: 480-483.	
6. Kristiansen, J.N. & Fox, A.D. Asymmetric insolation interception and consequences for leaf growth in <i>Deschampsia caespitosa</i> tussocks.	
7. Fox, A.D., Kristiansen, J.N., Stroud, D.A. & Boyd, H. 1998. The effects of simulated spring goose grazing on the growth rate and protein content of <i>Phleum pratense</i> leaves. <i>Oecologia</i> 116: 154-159.	
8. Kristiansen, J.N., Fox, A.D. & Nachman, G. 2000. Does size matter? Maximizing nutrient and biomass intake by shoot size selection amongst herbivorous geese. <i>Ardea</i> 88: 119-125.	

9. **Kristiansen, J.N., Fox, A.D., Boyd, H., Nyegaard, T. & Nachman, G.** The relationship between preferred food density and grazing White-fronted Geese: an example of an asymptotic aggregative response.
10. **Kristiansen, J.N., Fox, A.D. & Jarrett, N.S.** 1999. Resightings and recoveries of Canada Geese *Branta canadensis* ringed in West Greenland. *Wildfowl* 50: 199-203.
11. **Kristiansen, J.N. & Jarrett, N.S.** (accepted). Nest sites of the newly established Canada Goose population in West Greenland. (Dan. Orn. Tidsskr.)
12. **Kristiansen, J.N. & Jarrett, N.S.** Inter-specific competition between White-fronted and Canada Geese moulting in West Greenland; mechanisms and consequences. (submitted)
13. **Fox, A.D., Kahlert, J., Walsh, A.J., Stroud, D.A., Mitchell, C., Kristiansen, J.N. & Hansen, E.B.** 1998. Patterns of body mass change during moult in three different goose populations. *Wildfowl* 49: 45-56.
14. **Kristiansen, J.N. Fox, A.D., Kahlert, J. & Therkildsen, O.R.** Field methods to assess flight muscle volume in molting geese.

1. PREFACE

This thesis is the result of my three year Ph.D. project at the University of Copenhagen, Department of Population Ecology and the National Environmental Research Institute (NERI), Department of Coastal Zone Ecology. The project was funded by the University of Copenhagen, the Faculty of Science. Internal supervisors were Associate Professor Gösta Nachman and Emiretus Jan Dyck and external supervisor Senior Scientist Tony Fox, NERI.

Originally the aim of the project was to study competition between Greenland White-fronted and Canada Geese on the summering grounds in West Greenland. The Canada Goose has recently become established in parts of West Greenland and I saw this an outstanding opportunity to study inter-specific competition under natural conditions. However, the original project purpose had to be changed for various reasons. First, to study inter-specific competition, both sympatric and allopatric situations are needed. In the summers of 1996 and 1997 (before my Ph.D. was initiated), there were several sympatric sites within the Isunngua study area in West Greenland. In the summer of 1998, my first field season, only a single sympatric site was found. At this site non-breeding White-fronted and Canada Geese shared the same lake with surrounding feeding sites offering a suitable situation for studying the phenomenon of competition. Unfortunately no other sympatric breeding or brood-rearing sites were found despite intensive ground and aerial search effort that year and intensive aerial search the following year. Hence, further field studies on inter-specific competition were impossible. Furthermore, unfortunately I injured my ankle and had to cancel any further tough fieldwork in 1999 and 2000. Therefore, I was lucky to be involved in more gentle field studies of spring staging Greenland White-fronted Geese in Iceland and this work has subsequently been part of my Ph.D.

During the three years I have been lucky to meet and work with a number of stimulating and friendly people. Part of those collaborations have resulted in a number of publications. The once I have chosen not to include are listed below.

Kristiansen, J.N. (ed.) 1998. Greenland White-fronted Goose Study. Report of the 1997 expedition to Isunngua, West Greenland. Copenhagen. Pp 44.

Kristiansen, J.N. 1998 Grågæssenes redesteder In: Mortensen, P.H. (ed.). Vejlernes Natur – Satus 1998. 302 pp.

Kristiansen, J.N. & Eriksen, T. 1999. Rørdrummens præference for paukeplads i Vejlerne. Faglig Rapport fra DMU nr. 304. Pp. 75-77.

Kristiansen, J.N., Walsh, A.J., Fox, A.D., Boyd, H. & Stroud, D.A. 1999. Variation in the belly barings of Greenland White-fronted Goose *Anser albifrons flavirostris*. *Wildfowl* 50: 21-28.

Kristiansen, J.N. & Petersen, B.M. 2000. Remote sensing as a technique to assess reedbed suitability for nesting Greylag Geese. *Ardea* 88: 253-257.

Heldberg, H. & Kristiansen, J.N. 2000. Grønlandske canadagæs overvåges fra satellit. *Fugle og Natur* 3: 20-21.

Kristiansen, J.N. 2001. Greylag Geese. In J. Kear (ed.): *Ducks, Geese & Swans of the World*. Oxford University Press. *In press*.

Kristiansen, J.N. & Eriksen, T. Booming site selection of Bitterns *Botaurus stellaris* at Vejlerne, Denmark (submitted)

The Ph.D. thesis itself encompasses a short synopsis in which the background and the most important results are outlined. This is followed by 14 manuscripts, which form the main part of the thesis. The numbers of the manuscripts are referred to in the synopsis.

2. ACKNOWLEDGEMENTS

This thesis appears at first sight as the work of one person. However, without the help and co-operation of many friends and colleges this work would never have been accomplished. I am grateful to all the people who have helped in many ways during all the three years. Most of these have been thanked in each of the manuscripts. However, there some people I need to acknowledge further. First I owe Tony Fox tremendous thanks. He is the main reason for me becoming interested in goose research. I met Tony in 1994 and already there I was "infected" by his enthusiasm! He has always been a great support and inspiration not only as a supervisor but also as a very good friend all the way to the last minute of the project! I am extremely grateful to the lovely Fox-family; Tony, Anne, Gwen and Mia for providing accommodation during my many visits to Kalø. I thank Jan Dyck whom I have known for many years now and who has been a great inspiration and believer in my work. I am grateful to Gösta Nachman both for his support as a supervisor (especially concerning statistical problems!!) but also for his warm and friendly personality. I have had the privilege to work with Hugh Boyd during three seasons in Iceland. Every time my interest and enthusiasm in goose ecology has been strengthened due to many fruitful discussions and experiences together. I appreciate his open mind and patience and respect with a young and inexperienced goose researcher. I thank David Stroud whom I have had the pleasure to work with both in Greenland and in Iceland. His enthusiasm of the Greenland White-fronted Geese has always been highly stimulating. Alyn Walsh who is not only one of the most skilled field persons I have known but also a very warm a good friend, is thanked for many wonderful and exciting hours in the field. I met Nigel Jarrett on a ringing expedition to Greenland in 1997. Because of his tremendous interest in my work, his many years of field experience and personality, I asked him to assist me in Greenland the following year. I thank Nigel for one of the most fascinating and fruitful field experiences and for his subsequent co-operation and friendship. I also thank his lovely wife Stephanie Warren for her

kindness and for providing accommodation during my stays in the UK. I am grateful to a number of people during my stays in Iceland. Björn Þorsteinsson and his wife Anna Guðrún Þórhallsdóttir, The Agricultural College at Hvanneyri are thanked for their hospitality and for invaluable help during my stay at Hvanneyri. I am also grateful to Ríkharrð Brynjólfsson for his help and information of *Phleum* and I appreciate the help and patience of the staff at Hvanneyri. I owe Arnor Þ. Sigfusson and Óli Einarsson, Icelandic Institute of Natural History many thanks for all their help and support in Iceland. I thank David Boertmann, NERI and Claus Nygaard, Directorate of the Environment, Greenland for supporting my project and therefore helping to convince others of its value. I thank the Danish Polar Center and the Greenland Homerule for allowing me to carry out my fieldwork in the beautiful country of Greenland. I thank the always helpful staff at KISS, Kangerlussuaq, Greenland. I am very grateful to the Beckett Foundation and to Dansk Jagtforenings Jubilæumsfond for financial support. I thank the "goose people" at Kalø for their kindness and for stimulation discussions during my stays at Kalø. Due to the many kind and friendly people -students, guest researchers, technical staff, professor and lectures- at the Department of Population Ecology, I have spent many wonderful years at the University and I especially thank my "room mate" Timme Nyegaard for many happy and stimulating hours. Many thanks to Bill Neill for letting me use some of his beautiful drawings of Greenland White-fronted Geese for the cover of this thesis. Finally I am indebted to my lovely wife Regitze for her help, patience and tolerance especially during the final stages of the work.

3. SYNOPSIS

3.1 Introduction

Arctic breeding geese (*Branta* and *Anser*) are long distance migratory herbivorous birds. Their mobility enables the exploitation of different habitats at different times of the year to sustain them through particularly critical periods (e.g. those of enhanced nutrient and energy demands). The spring migration/spring staging (e.g. Ebbsing et al. 1982, Ebbsing 1989, Johnson & Sibly 1993) and the flightless moult (reviewed in Hohman et al. 1992) are such periods which are especially demanding for the birds in terms of resource (energy and nutrient) acquisition. In spring, northern nesting geese migrate northwards from generally temperate winter grounds to arctic breeding areas, where the short summer season offers abundant food, but no facility for winter survival. Hence, the birds have to gain sufficient energy (to fuel spring migration) and nutrients (e.g. to construct the necessary flight apparatus and egg-production) within a limited period of time. During the post-nesting moult, geese become flightless and are more susceptible to predation and restricted in choice of feeding area. At this time, geese require food both to sustain body maintenance and to meet the demands of protein synthesis. However, herbivores are generally agreed to be constrained to ingest relatively poor quality food (i.e. low metabolisable energy and low nitrogen, which characterises most green plant material) (Crawley 1983, 1997) which limits the ability of such organisms to rapidly accumulate energy and nutrients. Geese in particular are considered to possess inefficient digestive systems (Owen 1980). So it is not surprising to find that geese adopt a range of different behavioural strategies and adaptations in order to optimise their food intake to meet these requirements. Various factors may affect the foraging of the birds such as food abundance, food availability, food quality, predation and disturbance risk and competitive interactions (intra- and inter-specific).

In this thesis I focus upon some of these factors, which potentially affect the foraging efficiency of Greenland White-fronted Geese

Anser albifrons flavirostris during spring staging and the moulting period. In the study of spring staging, particular emphasis is placed on how geese maximise their intake during a brief stopover in Iceland en route to their breeding grounds. The recent colonisation of West Greenland by Canada Geese *Branta canadensis* have caused the potential for inter-specific competition between this new arriver and the Greenland White-fronted Goose and particular emphasis has been placed on inter-specific interactions between these two species during the flightless moult period.

This synopsis gives a brief overview and outlines the most important findings of the work.

The distinct race of the White-fronted Goose *A.a. flavirostris* –The Greenland White-fronted Goose– breeds in West Greenland and winters in Ireland and Scotland (Fig. 1). In mid April after having spent 5-6 months on the winter grounds the geese initiate their c. 3000 km journey towards their breeding grounds in West Greenland (Fox et al. 1994). The geese divide this journey into two parts, with a three week stopover in Iceland some 1500 km from the winter quarters in Ireland and Scotland and approximately half way to the breeding grounds. The journey from Iceland to Greenland (also c. 1500 km) is also demanding crossing open sea as well as climbing over the extensive inland ice cap of Greenland (c. 2800 m at its lowest point, Glahder et al. 1999). Such a climb is particularly costly for such a large bird (Gudmundsson et al. 1995). Therefore, they will not only have to replenish resources expended on the first part of the journey but potentially build up even more energy reserves than were necessary for the first part of the trip. On arrival in West Greenland (early May) the geese gather in certain lowland wetland areas, which offer the first access to food in spring (Glahder 1999). After c. two weeks of pre-nesting feeding, reproductive females commence nest-building and egg-laying followed by approximately one month of incubation where the females feed relatively little (Fox & Stroud 1988, Fox 2001).

After hatching, the young are moved by the parents to brood rearing areas and in early July the non-breeding element of the population gather in smaller flocks to moult their flight feathers (Stroud 1981, Glahder 1999). During the following three to four weeks the birds need protein for feather production (Hohman et al. 1992) and are due to being flightless especially susceptible to mammalian predators such as Arctic Foxes.



Fig. 1. Map of Greenland, Iceland, Britain and Ireland showing approximate breeding range, staging areas and wintering areas respectively of Greenland White-fronted Geese.

3.2 Iceland

Staging areas and phenology in spring and autumn (ms 1)

To assess the importance of Iceland as a staging site for migrating Greenland White-fronted Geese, surveys of the distribution and numbers supported by resightings and recoveries has taken place in 1986 (Francis & Fox 1987) and during 1990-1992 and 1997-1999 (ms 1). Two major staging areas used by the Greenland White-fronted Geese have been identified. The southern lowlands and the western lowlands (Fig 2). The core site in the western lowlands being Hvanneyri Agricultural College.

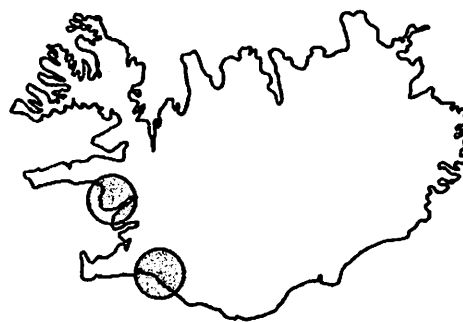


Fig. 2. Map of Iceland showing the two main staging areas for Greenland White-fronted Geese; the western and the southern lowlands.

In 1990-1992 in the southern lowlands the first birds arrived around mid April and along one count transect monitored each year gradually build up till c. 25 April with up 4-600 birds. After this peak there was a gradual decline and most had left around 9 May. In 1997-1999 in the western lowlands the first birds were also observed from mid April but contrary to the southern lowlands, there was rapid build up and at Hvanneyri a maximum of 1100-1500 birds were recorded 20-23 April. This was followed by a rapid decline to a more or less constant level with c. 600-1000 birds remaining the rest of the period. There is no exact information on the turnover of birds in the staging areas and hence the total number of birds passing through is unknown. However, from individually marked birds, individual geese seem to use different staging strategies. In the western lowlands approximately 50% of the birds that were resighted during 1997-1999 stayed for less than a week and more than one third stayed for the entire staging period (i.e. three weeks).

In autumn birds are recorded 30 August to 31 October and seem to be using the same staging areas as in spring, however we still know relatively little about the distribution and numbers of staging Whitefronts at this time of the year.

Staging site fidelity of Greenland White-fronted Geese in Iceland (ms 2)

Since 1986 individually marked Greenland White-fronted Geese have been resighted in Iceland. These records were used to assess individual site use by the geese in the main

staging areas (ms 2). In spring, at least 90% of goslings were associated with parents and siblings. Of these birds ringed as goslings, all were reported subsequently seen within 4 km of where they were first seen with their parents in spring. Of multiple within-spring resightings of 192 marked individuals, 96% were within 4 km of each other; 3 geese moved 88 km from the southern to the western staging areas. Four percent of the 45 marked geese seen in two consecutive springs and none of the 27 birds seen in consecutive autumns moved more than 4 km between years. By contrast, significantly more (12%) moved more than 4 km in subsequent seasons between spring/autumn and autumn/spring. All these individuals shifted to Hvanneyri Agricultural College in autumn, the only declared hunting-free area for Greenland White-fronted Geese. Based upon resighting histories and recoveries of shot birds, Scottish wintering birds were more likely to use the southern staging areas and Wexford (Ireland) wintering birds were more likely to be seen staging in the western lowlands. Given the apparent cultural reinforcement of patterns of use of staging areas in Iceland, the high levels of site loyalty and the relatively limited exchange between southern and western staging areas, we argue for strategic refuge designation throughout both staging areas adequately to protect the population.

Spring fattening (ms 3)

In order to assess the extent to which the staging Greenland White-fronted Geese accumulated stores for their onward migration during their stay in Iceland, we used two methods. First, large stores of fat can be deposited in the abdomen of geese (Thomas et al. 1983) thus the profile of the abdomen can be scored in the field (i.e. using abdominal profile index scores, API), and is a useful tool to assess the condition of a goose without necessitating its capture (Owen 1980, Madsen 1995, ms13). Sampling of API was carried out on the wintering grounds in Ireland prior to departure during 1990-1991 and 1997-

1998. In Iceland, apart from sampling of API in the western lowlands (Hvanneyri) during 1997 and 1998 sampling was also done in the southern lowlands during springs of 1990 and 1991. Second, geese were caught using cannon nets at intervals during the staging period in spring 1999 and individual geese were weighed and scored in the hand for their API.

Abdominal profiles were markedly lower on arrival in Iceland than at departure from Ireland in the same spring indicating a weight loss during the first part of the journey. Profiles generally increased from arrival (16-24 April) to departure (by 12 May), though there was variation between years and individuals. API scores from paired females started higher than males and increased more rapidly and pairs with broods tended to have larger profiles than those without. In 1998, other adults, confirmed or presumed to be offspring from earlier years, accompanied about 5% of pairs. These pairs, and the 'adults' accompanying them, also tended to have larger profiles than pairs without young.

In spring 1999 the body mass of birds caught during the staging period increased by c. 400 grams for both males and females (Fig. 3). In terms of energy stores required to sustain flight onwards to Greenland, this is in fact more than needed as estimated by Fox (2001) based on Pennycuicks (1989, using the most recent version of his software; Flight.bas version 1999) model of the energetic costs of flight for a Greenland White-fronted Goose and using still air range estimates from the literature. If the birds do put on more than needed for only the flight, then the excess could be allocated into reproduction or serve as a buffer for survival in case of severe weather condition on the breeding grounds on arrival as happened in 1984, when breeding was delayed c. three weeks due to snow cover (Fox & Stroud 1988).

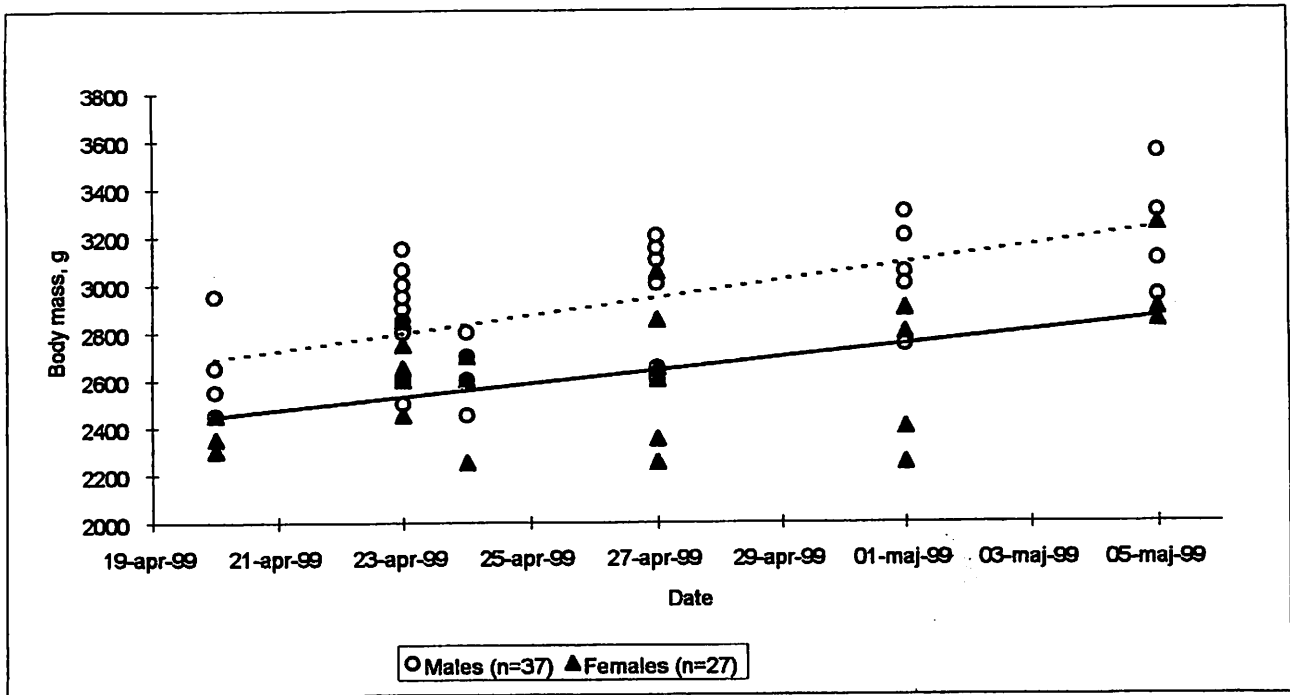


Fig. 3. Body mass increase of Greenland White-fronted Geese in Iceland during spring staging 1999 based on weights of captured birds (Nyegaard et al. in prep.).

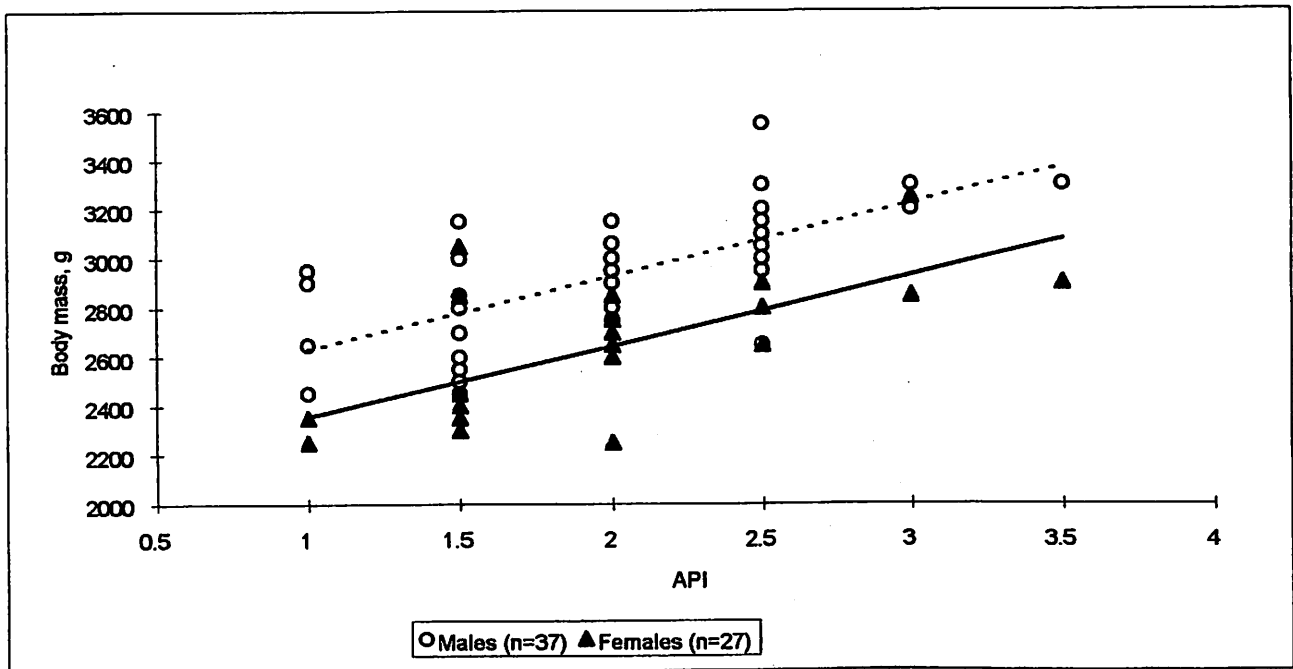


Fig. 4. Relationship between body mass, g and API score of Greenland White-fronted Geese in Iceland spring 1999 based on captured birds (Nyegaard et al. in prep.).

Fig. 4 shows the relationship between body mass and API of these birds. This confirms the positive relationship between body mass and API and shows that a weight increase of c. 300 grams is equivalent to a change in API-score of c. 1.

Feeding behaviour and food intake of Greenland White-fronted Geese (ms 4-9)

A high proportion of green ingested food comprises cell wall structure unavailable to the geese because of their relatively simple gut structure. Geese therefore rely upon high throughput of such food material and rapid absorption of readily digestible cell contents and for this reason must spend extended periods of time feeding (e.g. Owen 1972, Gauthier et al. 1988, Percival & Percival

1997). Prior to migration and breeding the need for nutrients and energy is especially high (Krapu & Reinecke 1992). During their spring staging preparing for the second part of

their journey, the Greenland White-fronted Geese in Iceland spend 70-90% of daylight hours feeding (Fig. 5).

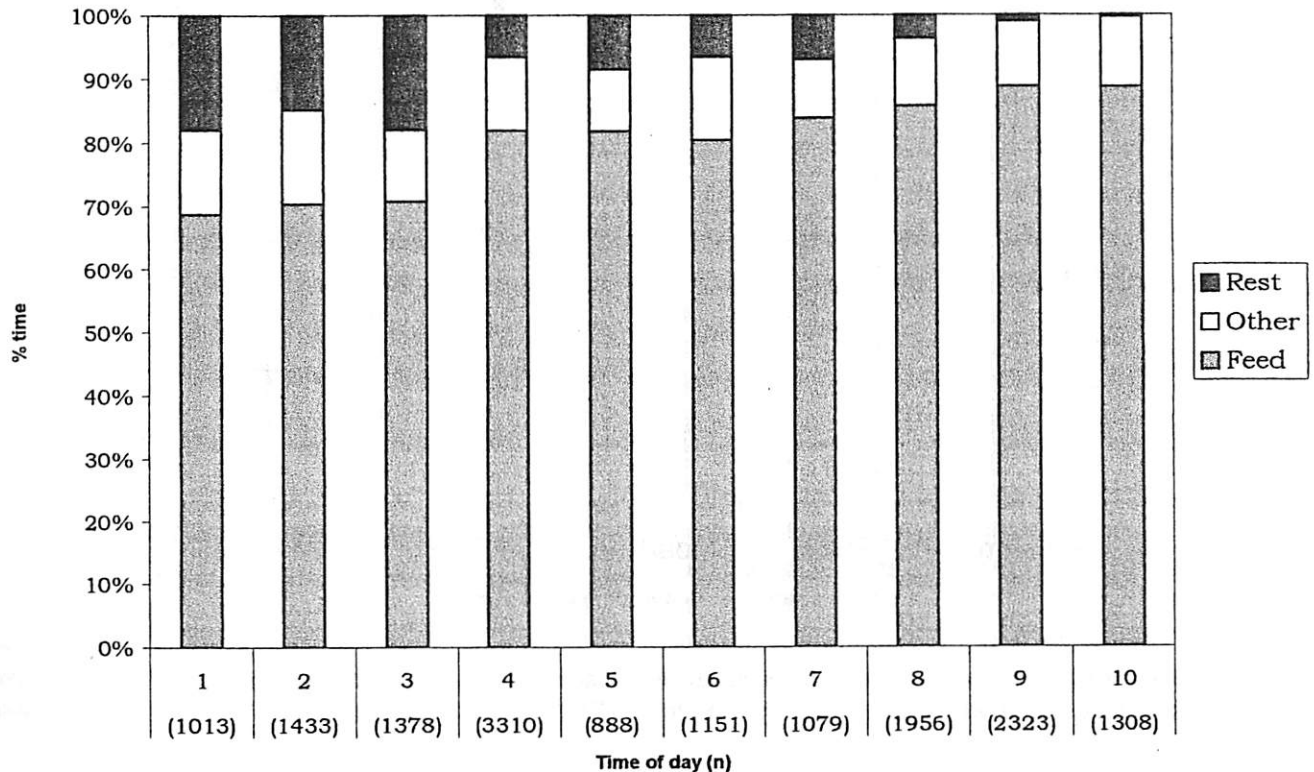


Fig. 5. Diurnal behavioural activities of Greenland White-fronted Geese in Iceland spring 1999. (Nyegaard et al. in prep.). Because of the change in sunrise and sunset during the study period, the time from the arrival of the first birds (10 minutes before sunrise) until they had left the fields (30 minutes after sunset) was divided into intervals of equal lengths.

It is clear that given the relative inefficiency of foraging on green food and the imperative to acquire sufficient fat and other stores for investment in the flight to Greenland and subsequent reproductive attempts, small differences in feeding efficiency could potentially have large consequences for foraging success of an individual. At Hvanneyri, for example, it is known that there are a range of different managed sward types in the hayfields used for feeding by the geese the predominant species being *Phleum*

pratense, *Poa pratense* and *Deschampsia caespitosa*. *Phleum*, which is an introduced species from Norway (Thorvaldsson 1996), needs to be reseeded regularly because of a gradual invasion over time by *Poa* and *Deschampsia* the two native species (Fox 1993). This will therefore also result in mixed swards. The geese responded to the different sward types in their density and grazing pattern (Fox 2001). The use of fields by geese showed that the different swards supported different levels of densities of geese over time *Phleum* > *Poa* > *Deschampsia* (Fig 6).

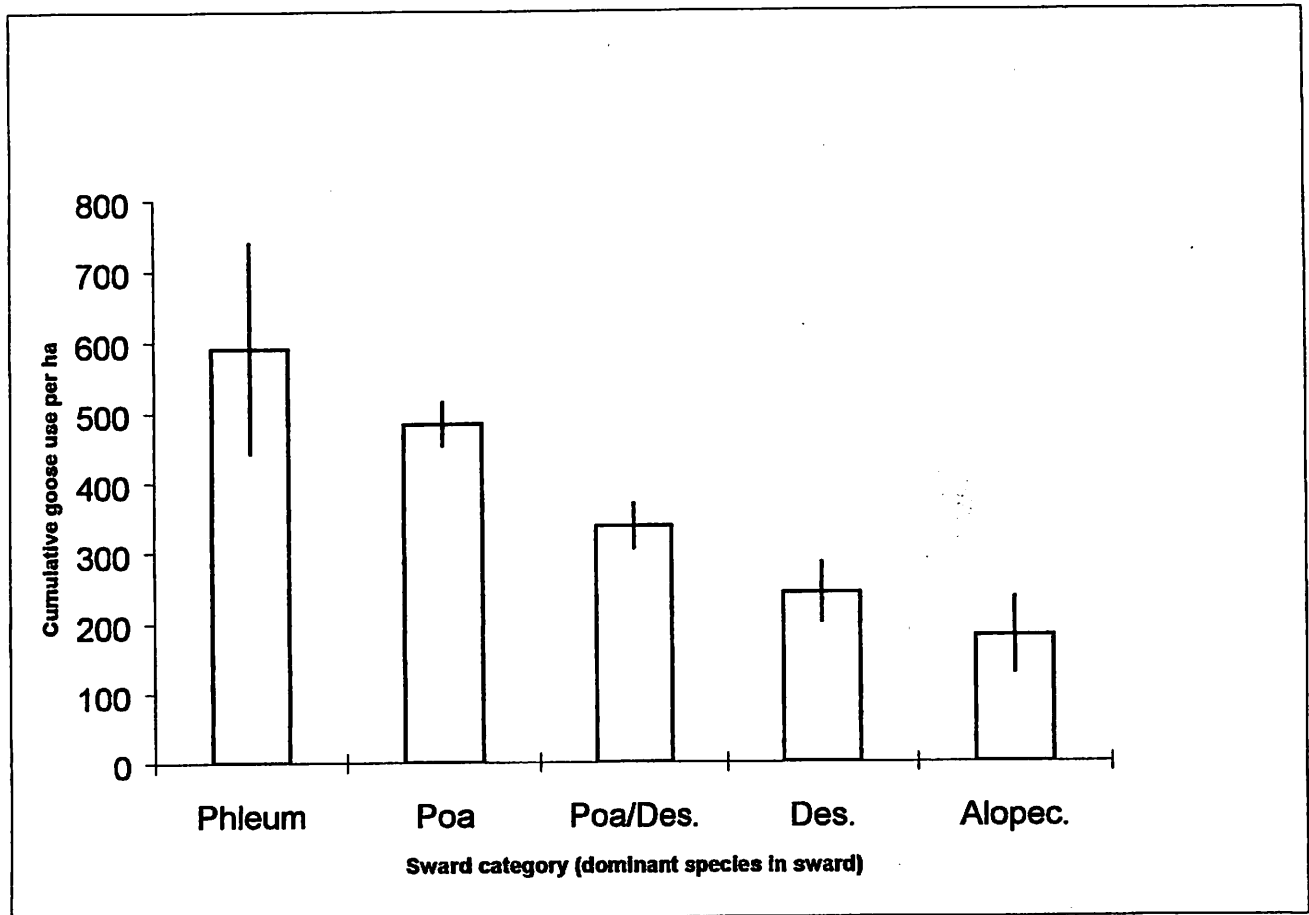


Fig. 6. Cumulative goose use of fields of different sward composition, expressed as total geese per hectare during the spring staging period at Hvanneyri (from Fox 2001). *Phleum pratense*, *Poa pratense*, *Deschampsia caespitosa* and *Alopecurus* sp.

An initial analysis suggested that the rate of change in API was also related to sward type (ms 3). The median profile scores of females feeding on swards dominated by *Poa pratense* increased more rapidly than those on *Deschampsia caespitosa*, though those of males did not. Unfortunately, *Phleum* dominated fields were not included in this study. However, feeding on *Phleum* dominated fields gave the birds the highest energy intake compared to the other sward types (Nyegaard et al. unpubl. data).

Since *Phleum* was the most preferred, I concentrated mainly on how geese assorted themselves with respect to this resource, how the geese specifically exploit this species and especially attempted to determine whether agonistic interactions might regulate access to

this preferred food. Hence, an attempt was made to determine the way foraging behaviour affected the ability of the individual to acquire nutrient and energy stores. Since geese are highly social animals, behavioural mechanisms were also investigated to determine their role in enhancing feeding efficiency of the geese on this particular resource. In particular, emphasis was placed upon how flock structure might offer costs (through interference) and benefits (through shared vigilance between greater numbers) to foraging efficiency during the staging period.

The benefit of mixed-species feeding (ms 4)
 Geese are highly gregarious which may benefit them in different ways. Being part a flock may enhance the search efficiency for good feeding sites and it may lower the

predation risk in two ways. First, the overall probability that an individual will be predated will decrease with increasing flock size, the so-called dilution effect (Krebs & Davies 1987). Second, the overall vigilance will increase with flock size such that an approaching predator is likely to be detected earlier (Krebs & Davies 1987). In Iceland we found that feeding White-fronted Geese lowered the amount of time spent vigilant by the individual but increased the overall level of vigilance with increasing flock size (ms 4). In addition, the White-fronted Geese often joined pairs of Greylag Geese in which the gander spent up to 70% of daylight hours alert attending his mate. Apparently the White-fronted Geese were aware of this and used this behaviour of the Greylag Geese to lower the time they spent alert and by that could allocate more time into feeding activities.

Microtopographical food selection (hummock aspect level) (ms 5-6)

Given the need to maximise throughput of their food, feeding geese are known to select those areas of highest profitability. Such a selection can manifest at several different spatial scales, from the part of the leaf selected to selection of a particular leaf, to species selection in order to maximise intake per bite (Fox 1993, Therkildsen & Madsen 2000). *Deschampsia caespitosa* is one of the grass species that the Greenland White-fronted Geese exploit in Icelandic hayfields (ms 5). This grass has a tussock growth form and when geese fed on these tussocks they grazed exclusively on the southern fringes of the tussocks. Due to different solar insulation and temperature differences between northern and southern fringes of the tussocks at this early time of the year, the southern fringes had significantly higher biomass and produced leaves with higher protein content than the northern fringes (ms 5-6). Hence, at the microtopographical scale, geese selected the most profitable part of the plant on which to feed.

Microtopographical food selection (leaf size) (ms 7-9)

Optimal foraging has been applied to a number of predators-prey systems, which have revealed that predators often select prey according to size, depending on the profitability of the particular prey. Geese select feeding sites on the sward level (Boudewijn 1984, Vickery et al. 1995), taking those plants of highest nutritious value (Madsen & Mortensen 1987, Fox et al. 1998). However, they also select the part of the plant of the highest nutritional value (Fox 1993, Therkildsen & Madsen 2000, ms 5). Because the White-fronted Geese in Iceland take only the middle erect youngest lamina of *Phleum* shoots we were able to investigate if these animals also selected at an even more fine-grained scale (ms 8). The geese selected only the larger laminae, avoiding the smaller ones. Usually one would expect a declining relative quality (protein content) with increasing size in the grass leaves. However, within the restricted size range of laminae in this study, there was no difference between the size classes, and thus by only taking the largest laminae gave the geese the highest nitrogen (protein) intake per peck. The preferred size classes were however dependant on the nature of the sward in each field. The field with high density provided generally much smaller shoots (and also laminae) and the geese selected smaller laminae on this field compared to the low and medium density fields on which average shoot size was larger thus offering the geese larger laminae.

The phenomenon of cyclical or sequential grazing by geese in which the birds switch between sites and keep returning to the same sites with some intervals has been demonstrated for Brent Geese *Branta bernicla* (Prins et al. 1980, Rowcliffe et al. 1995). A feeding site will be abandoned when the food resource has been depleted to a level in which the intake reaches a certain threshold. The time interval between visits will depend on the food plant species, that is the re-growth

rate and quality and of course also depend on alternative food resources in the vicinity. At the fields of the Agricultural College farm at Hvanneyri, one of the most important food plants is *Phleum pratense*. When feeding on this species the geese select almost exclusively for the middle youngest erect lamina. This enabled us to simulate goose grazing and mimic different types of sequential grazing using clipping experiments (ms 7). Cumulative counts of geese at *Phleum* dominated fields during the staging period revealed that the geese returned three to four times feeding for some days each time before leaving for another field. The growth rate of the laminae increased with clipping frequency and the experiment also showed increasing protein content with clipping frequency. Thus the plants that were cut 4 times provided the highest cumulative lamina elongation and the highest quality in terms of protein content. The conclusion was that by returning to graze on the same lamina four times during the three week period the geese gained 2.5 times more biomass and 3.5 times more protein than if they grazed each lamina only once during the staging period. This study only included the mechanical effect of clipping/grazing and did not take into account any additional fertilizer effect that the goose droppings might have given.

When the White-fronted Geese arrive in Iceland in mid April, the dominant available above ground green biomass is *Phleum pratense*. Hence, the distribution of grazing geese during the first part of the staging period is largely governed by the presence of this grass species (ms 9). The aggregative response (that is the relationship between consumer density and that of their food) showed that geese aggregated more as the density of *Phleum* shoots increased. However, at shoot densities above 10-20 shoots per 100 cm² an asymptotic level was reached. This lack of continued aggregation of consumers at high food density has usually been explained by an increase in aggressive encounters

among the consumers. In our study we found increasing aggression in one year but not in the other thus only partly supporting this hypothesis. Therefore, this alone may not explain the observed pattern. When examining the food more closely it turned out that lamina size decreased with increasing shoot density. From the study about lamina size selection we found that the geese selected laminae above a threshold level (ms 8). Therefore, this information was incorporated into this study and it turned out that at shoot densities between 10-80 shoots/100 cm² there was a constant number of laminae of preferred size. We therefore suggest that part of the underlying mechanisms responsible for the asymptotic nature of the aggregative of White-fronted Geese to their food may have been caused by this system.

Discussion

For arctic breeding geese the reproductive success of early arriving birds is higher compared to late arrivers (Cooke et al. 1995, Dalhaug et al. 1995). In addition, when departing the spring staging areas, the condition of the geese also affect the reproductive output such that birds departing in good condition have higher reproductive success than those in poorer condition (Ebbinge et al. 1982, 1989). Therefore, the importance of being first on the breeding grounds in good condition, forces the birds to gain large stores of energy and nutrients within a limited period of time on the spring staging areas. In order to do so geese may have to utilize different strategies. For instance, it is believed that the geese on their northward migration follow the growth phenology of their food plants because these are of high quality in the early growth (Drent et al. 1978).

The three-year work on spring staging Greenland White-fronted Geese in Iceland have provided additional information on how these birds optimise their intake. For instance, it has been demonstrated that the geese are

able to make small scale decisions at the blade level and how this may affect the way birds assort themselves at the field level in both space and time. Such detailed information about consumer/food relationship can therefore have management implications in terms of managing hayfields for geese.

In Iceland *Phleum pratense* benefit the Greenland White-fronted Geese in several ways compared to other grasses. 1) because of the earlier growth it allows the birds to arrive earlier, 2) it has a faster regrowth after grazing allowing the birds to return more frequently, thereby providing the birds with more cumulative biomass, 3) the quality (protein content) of the laminae increases with increasing grazing, also providing the birds with more cumulative protein and 4) it gives the birds the highest energy intake. This is all important, however, other food plant species (*Poa*, *Deschampsia* and underground parts of the sedge *Carex lyngbyei*), which are all exploited by the geese, may still have some importance providing the geese with other essential ingredients.

Only a minor part of the population returns to the wintering grounds in Ireland and Scotland with young (Fox 2001). Is this the result of individual strategies on the spring staging areas? In fact, there were differences in the rate of API increase of birds feeding on the different sward types and *Phleum* dominated fields were of highest quality in terms of energy acquisition (Nyegaard et al. in prep.). Furthermore, from individually marked birds there is evidence that some birds are site loyal to specific fields (i.e. *Phleum* specialists, *Poa* specialists and *Deschampsia* specialists) (Fox 2001). Therefore, future studies should focus more on individual feeding behaviour and strategies as individual decision of geese may have crucial importance at the population level.

3.3 Greenland

History of the Greenlandic Canada Geese Branta canadensis – a brief overview

In Western Greenland only the Greenland White-fronted Goose, historically occurred in the low arctic region (Salomonsen 1950, 1967, 1990, Boertmann & Glahder 1999). However, observations of Canada Geese *Branta canadensis* in this part of the country have been known since last century (Salomonsen 1950). Until recently these observations were mainly from the Disko Bay area (e.g. Salomonsen 1950, 1967, 1990, Frimer & Nielsen 1990, Boertmann 1994, Bennike 1990, Fox et al. 1996). The Canada Goose has now colonised several areas in the Disko Bay and is now locally more common than the Whitefronts (Bennike 1990). The expansion continues further south (Boertmann 1994, Fox et al. 1996 JNK pers. obs.) and in 1988 a survey of White-fronted Geese in the Isunngua area (67° 05'N, 50° 30'W) north of Søndre Strømfjord Airport (Kangerlussuaq), West Greenland found 12 Canada Geese including two fledged goslings. Relatively little increase occurred in that area the following six years (Fox et al. 1996) until in 1995 where more than 100 Canada Geese were found including several families (A.D. Fox pers. comm.). Similar numbers were observed in 1996 when the proportion of breeding pairs and goslings was even higher than previously (JNK pers. obs.). This increase is striking since numbers of Canada Geese now exceeds number of Whitefronts in the area. In addition, at some traditional Whitefront breeding sites only Canada Goose families were observed during the survey in 1996 (JNK pers. obs.). How would such a sudden occurrence and establishment of Canada Geese affect the Greenland White-fronted Geese in the area? The presence of both species in the Isunngua area offered a unique opportunity to study the phenomenon of inter-specific competition between two closely related species from the very beginning of expansion and immigration of the new arriver.

Canada Geese migration, wintering and origin (ms 10)

The origin, migration routes and wintering grounds of the Greenlandic Canada Geese have until recently been unknown. However, in 1992 and 1997 during ringing expeditions to Isunngua, West Greenland, Canada Geese were caught and marked, some with neck collars and some (downy goslings) only with metal leg rings. Subsequently, birds have been recovered shot from northern and central Labrador and New Brunswick, Canada during autumn. During winter the birds were recovered and resighted mainly in Connecticut, New York and Pennsylvania, USA. In 1999 six female breeders were caught and equipped with satellite transmitters and these birds also followed a straight line from the breeding grounds in West Greenland crossing the Davis Strait and Labrador to their wintering grounds in New York, Pennsylvania and Delaware (Duck Unlimited Homepage: www.ducks.org and Heldbjerg & Kristiansen 2000). Only two of the satellite birds survived the spring migration to the breeding grounds in 2000. These birds migrated northwards in a more or less straight line from Delaware to the very south-eastern point of Baffin Island, from which they change to a west north-westerly direction towards Isunngua, West Greenland where they spend the summer. This last part of their route may suggest that the Canada Geese in Greenland originated from southern Baffin Island (i.e. the subspecies *B.c. interior*) which was also supported by morphometric measurements of the birds that were captured in 1992 (Fox et al. 1996) and 1997 (ms 10).

Canada Goose nest sites (competition with Whitefronts?) (ms 11)

The density of geese in West Greenland is very low and it is often logistically difficult to get access to the areas where the geese are. Therefore, it is also difficult to find sufficient number of nests when trying to assess nest site selection of the two species. During fieldwork

1998 we found 14 Canada Goose nests used the present year but no Whitefront nests in Isunngua. Fortunately studies of Whitefronts c. 70 km further north had been carried out in 1979 and 1984 (Fox & Stroud 1988) which enabled us to make some comparison between the two species. Habitat characteristics were quite similar the main difference being that Canada Geese seemed to place their nests more exposed and much closer to the shore of lakes than the Whitefronts. This suggests that there might not be competition for actual nest sites, however, since these Canada Goose nests were located in the brood-rearing areas of the Whitefronts competition is very likely to occur when the Whitefronts bring their young to feed in these places.

Competition between moulting non-breeders (ms 12-14)

In West Greenland not only breeding geese of both species occur but also non-breeders spend the summer there. In early July these birds shed their flight feathers and are rendered flightless for c. four weeks until new feathers are re-grown (Glahder 1999b). During this period the birds undergo extreme physiological changes (review in Hohman et al. 1992, ms 13-14) and are highly selective for high quality food (especially protein Madsen & Mortensen 1987, Fox et al. 1998). We studied diet, behaviour and spatial distribution of non-breeding White-fronted and Canada Geese during moult in sympatry and in allopatry, in order to assess inter-specific competition (ms 12). In sympatry, the diet of White-fronted Geese comprised significantly higher content of low quality mosses compared to sympatric Canada Geese and both species in allopatry. White-fronted Geese in sympatry also showed a significantly broader diet (niche breadth) and lower ingestion rate than Canada Geese in sympatry and both species in allopatry. Sympatric White-fronted geese spent significantly more time feeding possibly to compensate for the low quality food and the low ingestion rate. Several physical inter-specific interactions

were recorded with White-fronted Geese being the inferior each time. In the study area, there was a dramatic increase of Canada Geese with a simultaneous decrease of White-fronted Geese during 1988-1998. These results suggest that inter-specific competition between Greenland White-fronted Geese and Canada Geese has occurred and maybe still occur in West Greenland.

Discussion

Our data suggest that the Canada Geese we have studied in West Greenland belong to the subspecies *B.c. interior*. However this may only be the case in the southern part of the distribution range. In fact there are indications that the smaller subspecies *B.c. hutchinsii* is most frequent in the northern part of the range (K. & A. Rosing-Asvid pers. obs., H. Ettrup pers. obs., Bennike 1990, and museum specimens from the Zoological of Copenhagen). The distribution of Canada Geese in North America according to Palmer (1976) and Bellrose (1976) showed that the *B.c. interior* was the most southerly distributed of the two subspecies extending from the Ungava peninsula to the southern tip of Baffin Island and that *B.c. hutchinsii* occurred slightly more to the north on Baffin Island. The apparent distribution of the two subspecies in Greenland is therefore what could be expected from this, *B.c. interior* as being the low arctic and *B.c. hutchinsii* the high arctic subspecies. However, we still need to clarify the details on subspecies distribution, the migration routes and wintering areas of *B.c. hutchinsii*. Future expeditions to the north-western Greenland therefore should attempt to catch and ring birds as well as attach satellite transmitters to these birds. In addition, blood samples should be taken to analyse DNA profiles as a help to clarify the subspecies question with more certainty. Apart from this, studies on competition between this smaller subspecies and the Greenland White-fronted Goose should also be carried out. Because larger species are more likely to out-compete

smaller species (Schoener 1983) our prediction would be that, in contrast to the *B.c. interior*, this small Canada Goose may be less successful than the Whitefronts. However, a study on Kent Peninsula, arctic Canada, found no indication of competition between *A.a. frontalis* and *B.c. hutchinsii* during pre-nesting feeding possibly due to differences in feeding techniques: The White-fronted Geese mainly grub for underground storage organs of plants whilst the Canada Geese mainly graze. This difference was probably caused by morphological differences in bill shape (Carrière 1996).

As a consequence of an enormous increase in most goose populations throughout the world it is expected that inter-specific competition would become an increasingly more important population regulating factor especially on the arctic summer quarters (Ebbinge 1985, Madsen 1987, 1991, Madsen et al. 1996, 1999). What we have witnessed in Greenland may well be the consequences of this. Our results suggest competition occurs at moulting sites and possibly also on the brood rearing areas. Another crucial period for these birds is the pre-breeding in which the geese (especially breeding females) feed intensively just after arrival in order to prepare themselves for egg laying and the long incubation. The birds exploit low lying areas which have thawed early offering the geese access to underground storage organs of their food plants (Fox & Madsen 1981). Such areas are probably sparse (Glahder 1999a) and therefore one would expect the potential for competition for these sites too. Although the information is limited, there is some indication that the Whitefronts arrive earlier than the Canada Geese hence giving them a competitive advantage over the later arriving Canada Geese.

The inter-specific competition between the Whitefronts and Canada Geese presented here might just be a snapshot occurring at a local scale. However, extensive aerial surveys in

1999 showed that Canada Geese and Whitefronts were distributed in the same latitudinal areas but were mutual exclusive at the local scale (Malecki et al. 2000). Since these species seem to use similar habitats, this may suggest that they avoid each other (competitive exclusion) at this local scale.

It is most likely that Canada Geese still have the potential to continue to increase and expanding their range both north and south of their present range. Yet, the total (winter) population of the Greenland White-fronted

Goose has not shown any clear decline although numbers have ceased increasing since 1995 (Madsen et al. 1999). The Greenland White-fronted Goose was considered threatened in the late 1970s but has since recovered (Fox et al. 1994). Therefore, despite the recovery, it is still important to monitor the population and follow the situation in Greenland as inter-specific competition may have the potential for becoming a threat to the population.

4. References

- Bennike, O. 1990. Observations of geese and other birds in West Greenland 1989 and 1990. *Dan. Orn. Foren. Tidsskr.* 84: 145-150.
- Bellrose, F.C. 1976. Ducks, Geese and Swans of North America. Harrisburg, Pa., Stackpole Books.
- Boertmann, D. 1994. An annotated checklist to the birds of Greenland. *Meddelser om Grønland, Bioscience* 38: 1-63.
- Boertmann, D. & Glahder, C.M. 1999. Grønlandske gåsebestande – en oversigt. Danmarks Miljøundersøgelser, Faglig Rapport fra DMU nr. 276., Denmark.
- Boudewijn, T. 1984. The role of digestibility in the selection of spring feeding sites by Brent Geese. *Wildfowl*, 35, 97-105.
- Carrère, S. 1996. Écologie de l'alimentation printanière chez des Anserinae (*Anser albifrons frontalis* et *Branta canadensis*) nichant en sympatrie dans l'Arctique. Ph.d. thesis. Université Laval, Québec, Canada.
- Cooke, F., Rockwell, R.F. & Lank, D.B. 1995. The Snow Geese of La Pérouse Bay. Natural selection in the wild. Oxford University Press.
- Crawley, M.J. 1983. Herbivory, the dynamics of plant and animal interactions. Blackwell, Oxford.
- Crawley, M.J. 1997. Plant Ecology. Blackwell, Oxford.
- Dalhaug, L. Tombre, I.M. & Erikstad, K.E. 1995. Seasonal decline in clutch size of the Barnacle Goose in Svalbard. *The Condor* 98: 42-47.
- Drent, R.H., Ebbinge, B. & Weijland, B. Breeding geese throughout the annual cycle: a progress report. *Verh. Orn. Ges. Bayern* 23: 239-264.
- Ebbinge, B., St. Joseph, L.A., Prokosch, P., Spaans, B. 1982. The importance of spring staging areas for arctic breeding geese, wintering in Western Europe. *Aquila* 89: 249-258.
- Ebbinge, B. 1985. Factors determining the population size of arctic breeding geese, wintering in Western Europe. *Ardea* 73: 121-128.
- Ebbinge, B. 1989. A multifactorial explanation for variation in breeding performance of Brent Geese *Branta bernicla*. *Ibis* 131: 196-204.
- Fox, A.D. 1993. Pre-nesting feeding selectivity of Pink-footed geese *Anser brachyrhynchus* in artificial grassland. *Ibis* 135: 417-422.
- Fox, A.D. & Madsen, J. 1981. The pre-nesting behaviour of the Greenland White-fronted Goose. *Wildfowl* 32: 48-54.
- Fox, A.D. & Stroud, D.A. 1988. The breeding biology of the Greenland White-fronted Goose *Anser albifrons flavirostris*. *Meddelser om Grønland, Bioscience* 27: 1-14.
- Fox, A.D. Norriss, D.W., Stroud, D. and Wilson, H.J. 1994. Greenland white-fronted geese in Ireland and Britain 1982/83-1993/94. Greenland White-fronted Goose Study Research Report No. 8. GWGS/NPWS, Aberystwyth and Dublin.
- Fox, A.D., Glahder, C., Mitchell, C.R., Stroud, D.A., Boyd, H. & Frikke, J. 1996. North American Canada Geese (*Branta canadensis*) in West Greenland. *The Auk* 113: 231-233.

- Fox, A.D., Kahlert, J. & Ettrup, H. 1998. Diet and habitat use of moulting Greylag Geese *Anser anser* on the Danish island of Saltholm. *Ibis* 140: 676-683.
- Fox, A.D. 2001. The Greenland White-fronted Goose and its annual cycle; a migratory herbivore on the continental fringe. Doktordisputats. National Environmental Research Institute, Denmark.
- Francis, I.S. & Fox, A.D. (1987) Spring migration of Greenland White-fronted Geese through Iceland. *Wildfowl* 38: 7-12.
- Frimer, O. & Nielsen S.M. 1990. Bird observations in Aqajarua-Sullorsuaq, Disko, West Greenland, 1989. *Dan. Orn. Foren. Tidsskr.* 84: 151-158.
- Gauthier, G., Bédard, Y. & Bédard, J. 1988. Habitat use and activity budgets of Greater Snow Geese in spring. *Journal of Wildlife Management* 52: 191-201.
- Glahder, C.M. 1999a. Spring staging areas of the Greenland White-fronted Goose *Anser albifrons flavirostris* in West Greenland. *Arctic* 52: 244-256.
- Glahder, C.M. 1999b. Sensitive areas and periods of the Greenland White-fronted Goose in West Greenland; spring staging and moult as important bottleneck periods in the annual cycle of the goose species. Ph.D-thesis. Ministry of Environment and Energy, National Environmental Institute, Denmark. 142 pp.
- Gudmundsson, G.A., Benvenuti, S., Alerstam, T., Papi, F., Lilliendahl, K. & Åkesson, S. 1995. Examining the limits of flight and orientation performance: satellite tracking of brent geese migrating across the Greenland ice-cap. *Proc. R. Soc. Lond.* 261: 73-79.
- Heldberg, H.C. & Kristiansen, J.N. 2000. Grønlandske Canadagæs overvåges fra satellit. *Fugle og Natur* 3: 20-21.
- Hohman, W.L., Ankney, C.D., Gordon, D.H. 1992. Ecology and management of post-breeding waterfowl. - In: Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. and Krapu, G.L. (eds.) *Ecology and management of breeding waterfowl*: University of Minnesota Press, Minneapolis: 128-189.
- Johnson, I.P. & Sibly, R.M. 1993. Pre-breeding behaviour affects condition, assessed by abdominal profile, and hence breeding success of Canada Geese *Branta canadensis*. *Wildfowl* 44: 60-68.
- Krapu G.L. & K.J. Reinecke 1992. Foraging ecology and nutrition. - In: Batt, B.D.J., Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec and G.L. Krapu (eds) *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis: 1-29.
- Krebs, J.R. & Davies, N.B. 1987. An introduction to behavioural ecology (2nd ed.). Blackwell Scientific Publications, London.
- Madsen, J. 1991. Status of goose populations in the Western Palearctic in the 1980's. *Ardea* 79: 113-122.
- Madsen, J. 1987. Status and management of goose populations in Europe, with special reference to populations resting and breeding in Denmark. *Danish Review of Game Biology* 12(4): 1-76.
- Madsen J. & C.E. Mortensen 1987. Habitat exploitation and interspecific competition of moulting geese in East Greenland. *Ibis* 129: 25-44.

- Madsen, J., Reed, A. & Andreev, A. 1996. Status and trends of geese (*Anser* sp., *Branta* sp.) in the world: a review, updating and evaluation. In: Birkan, M. van Vessem, J., Havet, P., Madsen, J., Trollet, B. & Moser, M. (Eds.) Proceedings of Anatidae 2000 conference, Strasbourg, France, 5-9 December 1994. *Gibier Faune Sauvage, Game and Wildlife* 13: 337-353.
- Madsen, J., Cracknell, G. & Fox, T. (eds.) 1999. Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International Publ. No. 48, Wetlands International, Wageningen, The Netherlands. National Environmental Institute, Rønde, Denmark. 344 pp.
- Malacki, R., Fox, A.D. & Batt, B.D.C. 2000. An aerial survey of nesting White-fronted and Canada Geese in Western Greenland. *Wildfowl* 51:
- Owen, M. 1972. Some factors affecting food intake and selection in White-fronted Geese. *J. Anim. Ecol.* 41: 79-92.
- Owen, M. 1980. Wild geese of the world: their life history and ecology. B.T. Batsford, London.
- Owen, M. 1981. Abdominal profile - condition index for wild geese in the field. *J. Wildl. Manage.* 45: 227-230.
- Palmer, R.S. (Ed.). 1976. Handbook of North American Birds, vol. 2. Yale Univ. Press, New Haven, Connecticut.
- Percival, S.M. & Percival, 1997. Feeding ecology of barnacle geese on their spring staging grounds in northern Iceland. *Ecography* 20: 461-465.
- Prins, H.H.T., Ydenberg, R.C. & Drent, R.H. 1980. The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging. *Acta Bot. Neerl.* 29: 585-596.
- Rowcliffe, J.M., Watkinson, A.R., Sutherland, W.J. & Vickery, J.A. 1995. Cyclical winter grazing patterns in brent geese and the regrowth of salt-marsh grass. *Funct. Ecol.* 9: 931-941.
- Salomonsen, F. 1950. Grønlands Fugle. The birds of Greenland. Munksgaard, København.
- Salomonsen, F. 1967. Fuglene på Grønland. Rhodos. København.
- Salomonsen, F. 1990. Fugle Pp. 161-360. In: Salomonsen, F. (ed.) Grønlands Fauna. - Gyldendal, København.
- Schoener, T.W. 1983. Field experiments on inter-specific competition. *The American Naturalist* 122: 240-285.
- Stroud, D.A. 1981. Goose studies. In Fox, A.D. & Stroud, D.A. (eds.) Report of the 1979 Greenland White-fronted Goose study expedition to Eqaungmiut Nūnat, West Greenland. GWFG, Aberystwyth. Pp. 51-62.
- Therkildsen, O.R. & Madsen, J. 1999. Goose grazing selectivity along a depletion gradient. *Ecography* 22: 516-520.
- Thomas, V.G., Mainguy, S.K. & Pevett, J.P. 1983. Predicting fat content from abdominal fat weight. *J. Wildl. Manage.* 47: 1115-1119.
- Thorvaldsson, G. 1996. Botanical composition of Icelandic grass fields. *Acta Agriculturae Scandinavica Section B Soil Plant Science* 46: 121-127.
- Vickery, J.A., Sutherland, W.J., Watkinson, A.R., Lane, S.J. & Rowcliffe, J.M. 1995. Habitat switching by Dark-bellied Brent Geese *Branta bernicla bernicla* in relation to food depletion. *Oecologia* 103: 499-508.

**Phenology and distribution of Greenland White-fronted
Geese *Anser albifrons flavirostris* staging in Iceland**

**Fox, A.D., Hilmarsson, J.Ó., Einarsson, Ó., Boyd, H., Kristiansen, J.N., Stroud,
D.A., Walsh, A.J., Warren, S.M., Mitchell, C., Francis, I.S. & Nyegaard, T.**

1999

Wildfowl 50: 29-43.

**Staging site fidelity of Greenland White-fronted Geese in
Iceland**

Fox, A.D., Hilmarsson, J.Ó., Einarsson, Ó., Walsh, A.J., Boyd, H., Kristiansen, J.N.

Accepted

Bird Study

Changes in abdominal profiles of Greenland White-fronted Geese during spring staging in Iceland

Boyd, H., Fox, A.D., Kristiansen, J.N., Stroud, D.A., Walsh, A.J. & Warren, S.M.

1998

Wildfowl 49: 57-71.

**Greenland White-fronted Geese *Anser albifrons*
flavirostris benefit from feeding in mixed-species flocks**

Kristiansen, J.N., Fox, A.D., Boyd, H. & Stroud, D.A

2000

Ibis 142: 142-144.

**Dietary and microtopographical selectivity of Greenland
White-fronted Geese feeding on Icelandic hayfields**

Kristiansen, J.N., Fox, A.D., Stroud, D.A. & Boyd, H.

1998

Ecography 21: 480-483.

**Asymmetric insolation interception and consequences for
leaf growth in *Deschampsia caespitosa* tussocks**

Kristiansen, J.N. & Fox, A.D.

The effects of simulated spring goose grazing on the growth rate and protein content of *Phleum pratense* leaves

Fox, A.D., Kristiansen, J.N., Stroud, D.A. & Boyd, H.

1998

Oecologia 116: 154-159.

Does size matter? Maximizing nutrient and biomass intake by shoot size selection amongst herbivorous geese

Kristiansen, J.N., Fox, A.D. & Nachman, G.

2000

Ardea 88: 119-125.

The relationship between preferred food density and grazing White-fronted Geese: an example of an asymptotic aggregative response.

Kristiansen, J.N., Fox, A.D., Boyd, H., Nyegaard, T. & Nachman, G.

Resightings and recoveries of Canada Geese *Branta canadensis* ringed in West Greenland

Kristiansen, J.N., Fox, A.D. & Jarrett, N.S.

1999

Wildfowl 50: 199-203.

**Nest sites of the newly established Canada Goose
population in West Greenland**

Kristiansen, J.N. & Jarrett, N.S.

Accepted

Dansk Ornitologisk Forenings Tidsskrift

**Inter-specific competition between White-fronted and
Canada Geese moulting in West Greenland; mechanisms
and consequences**

Kristiansen, J.N. & Jarrett, N.S.

**Patterns of body mass change during moult in three
different goose populations**

**Fox, A.D., Kahlert, J., Walsh, A.J., Stroud, D.A., Mitchell, C., Kristiansen, J.N. &
Hansen, E.B.**

1998

Wildfowl 49: 45-56

**Field methods to assess flight muscle volume in molting
geese.**

Kristiansen, J.N., Fox, A.D., Kahlert, J. & Therkildsen, O.R.