

ENVIRONMENTAL BIOLOGY RESEARCH PROJECT

**Inter-Specific Competition and Habitat Exploitation of Moulting Geese in
West Greenland**

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PREFACE

This dissertation is concerned with an investigation of inter-specific competition between two species of geese, which moult in the same areas of West Greenland. In order to meet the requirements of AES 395 (Environmental Biology Research Project), the manuscript has an extended introduction in which the scientific literature dealing with competition between species of wildfowl is reviewed. In effect, this review sets the scene for the subject of the research project which is subsequently presented in the form of a scientific paper.

Inter-specific competition and habitat exploitation of moulting geese in West Greenland

1. ABSTRACT

In recent years, Canada Geese Branta canadensis interior have successfully established in areas of West Greenland previously only exploited by Greenland White-fronted Geese Anser albifrons flavirostris. In this study, diet, behaviour and spatial distribution of non-breeding, moulting White-fronted and Canada Geese, in sympatry and in allopatry, were investigated. In sympatry, the diet of White-fronts, assessed by analysis of faeces, comprised a high content of low protein Bryophyta species (22%). In contrast, sympatric Canada Geese showed a low content of Bryophyta species in their diet. Several physical interspecific encounters were recorded with White-fronted Geese being the inferior species each time. This study concludes that inter-specific competition (interference) does occur between non-breeding White-fronted and Canada Geese during their moult in West Greenland.

2. INTRODUCTION

It is a principle of ecology that whenever resources are in short supply, species with identical requirements cannot persist together indefinitely (Gause, 1934; Begon *et al.*, 1996). Inter-specific competition, defined as the joint use of a limited resource by two or more species (Pianka, 1976), is often portrayed as an evolutionary driving force, leading to species divergence and influencing the composition and structure of communities (MacArthur, 1972; Wiens, 1989; Nudds, 1992; Begon *et al.*, 1996). A resource may be food, breeding sites, predator free-space, etc.; indeed any one of the dimensions defining the niche of a species. Usually the effects of inter-specific competition are asymmetric, affecting one species more heavily than the other (Charnov *et al.*, 1976; Newton, 1998). Those species which are best adapted, or most efficient at exploiting a limiting resource, invariably out-compete others, and as a result species show differences in distribution, habitat-use or feeding ecology (Lack, 1947, 1971). Consequently, competition is characterised by individuals of one species suffering reduced fecundity, survivorship or growth as a result of resource exploitation or interference by individuals of other species (Begon *et al.*, 1996).

Exploitation or scramble competition, refers to the effects of indirect interactions caused by individuals of one species using resources and thereby reducing the amount available to their competitors (Schoener, 1983). Sutherland & Allport (1994) invoked exploitation competition to explain local feeding distributions of Wigeon *Anas penelope* and Bean Geese *Anser fabalis* wintering in East Anglia in England. Both species are herbivorous and graze grass and forb species managed on agricultural land. Companies of Wigeon arriving in September (ahead of goose flocks), settle to feed on swards set-aside especially for the geese. The ducks crop the sward very close to the ground and in so doing, they 'force' the October arriving geese to

seek alternative feeding opportunities, often in pastures away from the reserve. Mayhew & Houston (1999) have since shown that Wigeon actually maintain pastures as ‘grazing lawns’ by sequentially cropping new growth through the winter months. As a side effect, large, domestic herbivores are deprived use of winter productivity, but the effect on these ‘out-competed’ species’ fitness has yet to be demonstrated.

Interference competition occurs when one species physically excludes another from access to one or more resources (Schoener, 1983). Aggressive territorial behaviour is a form of interference competition, and although inter-specific territoriality is rare in birds (Krapu & Reinecke, 1992) it has been described as the cause for observed allopatry in species of ducks of the genus *Bucephala* (Savard, 1984). Studies of the Barrow’s goldeneye *Bucephala islandica* have indicated that interference behaviour functions specifically to reduce competition for food: the degree of aggression shown by male goldeneyes is strongly correlated to the degree of potential dietary overlap with the intruding species (Savard & Smith, 1987; Savard, 1988).

The outcome of competition will often manifest in terms of niche shifts along one or more of the dimensions defining the species’ niche, although the shift along only one dimension may be sufficient to reduce competition and its assumed negative consequences on fitness (Clode & Macdonald, 1995). Evidence of competition (e.g. for food) between two species can be obtained by comparing their ‘actual’ niche breadth (realised niche) e.g. dietary variation in sympatric populations (Clode & Macdonald, 1995). Thus, evidence for competition often comes from the contraction of a fundamental niche in the presence of a competitor, or from niche expansion in the competitor’s absence (Begon *et al.*, 1996).

The effects of inter-specific competition have been elegantly portrayed in number of laboratory- and field-based experiments, where ‘treatments’ have been carefully controlled (Connell, 1983; Schoener, 1983). Thus treatment effects may indicate competition in a measurable way, for example changes in feeding-rates (or niche shifts) or by changes in individual performances (survival, growth or fecundity). Laboratory based examples of experimental demonstrations of competition include the work of Park (1954) who demonstrated, that two species of flour beetle (*Tribolium castaneum* and *T. confusum*) were able to exclude one another competitively at different extremes of environmental temperature and humidity. In a series of field-based ‘removal experiments’, Connell (1961), showed that the barnacle *Balanus balanoides* actively excluded *Cthamalus stellatus*, by interference, from all but the upper zones of the sea-shore.

While these types of experiments enable hypotheses about competitive interactions to be rigorously tested, ecologists have often relied on other, often less than convincing and sometimes controversial, interpretations of observational data as evidence for competition (e.g. Lack, 1974). Huey (1979), partitioned evidence about competition in to three types: Types I, II and III. A description and review of each type of evidence follows with reference to the wildfowl literature.

2.1. Type I Evidence

Type I evidence for the presence or potential for inter-specific competition includes mere documentation of the fact that co-existing species exhibit differences in ecology or morphology (Huey, 1979). For example, Lack (1974) observed that co-existing wildfowl species used resources in different ways and explained the inter-specific variations as

responses to competition. He suggested that in the past, competitive exclusion of some species by other species, produced the ecological differences apparent in co-existing species today. Of course Type I evidence of this sort overlooks the possibility that differences between sympatric species may have evolved in allopatry without inter-specific competition ever operating. Inter-specific differences masquerading as Type I evidence include differences in feeding ecology and ecomorphology and these are considered separately below.

2.1.1. Feeding ecology

Early studies of the diet of ducks, geese and swans were based on post-mortem examination of guts and gizzards. Invariably, biologists concluded that different species of waterfowl had different, predominantly vegetarian diets (e.g. Cottam, 1939; Coulter, 1959) leading to inferences about competition (e.g. Lack, 1974). Later studies focused on diet as reflected by the contents of birds' oesophagi and fore-gut regions. These showed that not only did duck species consume more animal food than previously thought (e.g. Swanson *et al.*, 1979) but that there was often large dietary overlap, especially among ducklings of different species (Nudds, 1992). However, closer attention to the dietary items revealed that species' diet differed in terms of prey size and that the size of preferred prey correlated with the density of the lamellae on birds' beaks (Nudds & Bowlby, 1984). This latter study provides data which may be interpreted as Type I evidence for competition.

2.1.2. Ecomorphology

Type I evidence about competition has been inferred from differences in the morphology of co-existing animal species. Lack (1974), suggested that competition had been the evolutionary driving force producing variations in morphology (and feeding ecology) of six

species of Australian ducks. Nudds & Bowlby (1984) demonstrated that foraging behaviour, morphology and diet of North American dabbling ducks were correlated, and this study invited suggestion that these may have evolved as a consequence of competition (Nudds, 1992). Barnes & Thomas (1987) examined the digestive tracts of 22 species of wildfowl and correlated external differences with internal differences and suggested that there were possibly inter-specific differences in efficiency of resource extraction (that is, in terms of digestion).

Hutchinson (1959) observed that the anatomy of related species living in the same area sometimes differed by a constant ratio. Thus Hutchinson's Rule expects the morphology of competing species to differ predictably. Therefore body size may be used to provide Type I evidence for competition (Huey, 1979), since the size difference factor is thought to have evolved through natural selection operating to reduce inter-specific dietary overlaps (Nudds 1992). While Wiens & Rotenberry (1981) contradicted the rule for groups of co-existing species where size differences existed and where dietary overlap was large, Nudds *et al.* (1981) found size differences for wildfowl species that were consistent with Hutchinson's Rule.

It is clear that Type I evidence relies on observations that are difficult to test rigorously and which therefore, are only weakly indicative of competition. It is generally, but not universally, accepted that ecological differentiation alone, can not be used to support nor refute the existence of inter-specific competition (Nudds, 1992).

2.2. Type II Evidence

Type II evidence is considered to be stronger than Type I evidence, and often relies on data showing correlation between presumed changes in the intensity of competition and changes in the amount of differences among co-existing species. In wildfowl species, Type II evidence is often discussed in the context of niche complementarity, niche overlap or changes in population size. Examples of each are considered below.

2.2.1. Niche complementarity

The niche complementarity theory states that species that are similar in some aspects of their ecological requirements must differ in others if they are to co-exist (Schoener, 1974). Niche complementarity occurs most often along spatially governed niche dimensions (e.g. habitat-use and food choice), and less often along a temporal dimensions (Begon *et al.*, 1996).

Nevertheless, it is not unlikely that niche separation in time would be selected as a strategy if the costs of inter-specific competition were reduced (Toft *et al.*, 1982). Lack (1974) described three types of niche complementarity apparent in groups of wildfowl species, noting that:

1. Some species use similar habitats but have different geographical ranges. For example: European White-fronted Geese *Anser albifrons albifrons*, Greenland White-fronted Geese *A. albifrons flavirostris* and Greylag Geese *A. anser anser*, all occur in the UK where they graze on pastures **but** barely overlap in geographical range.
2. Some species eat similar food but obtain their diet from different habitats. Thus, complementarity can be observed at a local scale. Again referring to geese, Lack noted that four species (the White-fronted, the Pink-footed *Anser brachyrhynchus*, the Barnacle *Branta leucopsis* and the Brent Goose, *B. bernica*) all had similar foraging behaviour and

geographical range **but** each graze in different habitats with slight difference in diet occurring by virtue of feeding in the different habitats.

3. Some species use the same habitat but have different food preferences. Lack observed this type of complementarity in guilds of dabbling ducks where species foraged in the same wetland habitats but ingested different foods.

Closer examinations of species' ecology have shown that while dabbling ducks overlap considerably in habitat use, they finely partition micro-habitats, particularly the water depth at which food is collected (Pöysä, 1983a, 1983b, 1986). Dietary differences therefore result from different micro-habitat use, and reflect the distribution of food within the habitat. For example, invertebrates are an important dietary item of dabbling ducks and the size of preferred prey varies between duck species. Nudds (1992) demonstrated that prey item size varied with water depth, i.e. prey size decreased as the water column was descended. Siegfried (1976) also observed that diving ducks obtained very similar diets, but from different parts of the same prairie pothole wetlands of western Canada.

Observations that ducks with similar body size have allopatric breeding distributions may also be interpreted as a form of niche complementarity (Nudds *et al.*, 1981). Niche complementarity is also apparent in the demonstration that dabbling wildfowl species exhibit inverse relationships between similarities in body size and similarities in foraging behaviour Eadie *et al.* (1979). Pöysä (1983a) showed that dabbling ducks feeding at similar depths differed more in bill morphology than did those feeding at different depths, further exemplifying niche complementarity in guilds of wildfowl.

2.2.2. Niche overlap

The niche overlap theory (Pianka, 1976) predicts a positive relationship between species diversity and niche separation. Thus, where species compete for limited resources, species diversity may persist if niches are differentiated. Nudds (1983) demonstrated that diving ducks of the genus *Aythya* living in the aspen parkland of Alberta showed a positive correlation between niche separation and diversity as measured by Simpson's Index. However, this relationship was not apparent for dabbling ducks (genus *Anas*) at the same wetland sites.

While the niche overlap theory presumes that competition is a major driving force for niche contraction, factors, such as increased availability of resources, may also induce specialisation apparent as niche contraction. Consequently measurable increases in diversity may result from tighter niche packing. Similarly competition may not explain niche separation in communities of mixed species populations in which there is high density independent mortality (Abrams, 1977).

2.2.3. Changes in population size

If competition occurs it may be expected that population sizes of competing bird species will be inversely correlated in time and space (Newton, 1998). Nudds (1981) could not find an inverse correlation between the population sizes of coot *Fulica americana* and 10 species of ducks (using 26 years of consecutive census data) from which inter-specific competition between species could be inferred. Likewise, Brandl and Schmidtke (1983) found that Bavarian population densities of tufted duck and pochard were not negatively correlated. Nudds (1992) warned that observations of inverse density relationships do not indicate competition alone, and may have alternative explanations. The range expansion of the

mallard *Anas platyrhynchos* into the north-east USA was once presumed to be the cause and effect of a declining Black duck *Anas rubripes* population. However, habitat change is known to have played no small part in the recent fortunes of both species (Ankney *et al.*, 1987; Jarrett, *in press*).

2.3. Type III Evidence

Type III evidence about competition may be obtained from studies of the before and after effects of controlled treatments, or alternatively, from investigations of natural experiments. Natural experiments include those where competition can be inferred from the responses of species to changes in the intensity of the competitive mechanism. Where individuals of a species are added to or are removed from a system, the effects on other individuals of other species, manifested as niche shifts, may be measurable. Such niche shifts may be apparent in ecological time with respect to changes in habitat use or diet, or in evolutionary time with respect to morphological changes or character displacement. Niche shifts were described by Pöysä (1985) for Shovelers *Anas clypeata* feeding in association with Teal: when alone, Shovelers fed from the water's surface, but in the presence of Teal they altered their behaviour to feed with head and neck submerged. This appeared to be a direct response to short-term depressions in food quantities in the upper water layers.

Interference and exploitation competition caused Barnacle Geese to shift their feeding niche when in the presence of Pink-footed Geese, on moulting sites in East Greenland (Madsen & Mortensen, 1987). When separate, both species foraged for grasses and sedges (Poaceae), but where they fed together, both species ingested more moss, Barnacle Geese more so than Pink-feet. In allopatric situations, both species spent 41-46% of the arctic daytime grazing.

When they occurred together, the feeding duration of Pink-feet was unchanged but the grazing time of Barnacle Geese increased to 62%. Therefore both species were competing for the same resources, and the smaller Barnacle Goose appeared to 'suffer' more than the Pink-footed Goose in mixed flock situations. Aggressive interference was recorded on one occasion: a flock of Pink-footed Geese excluded Barnacle Geese from a favoured riverine grazing area. The effects of competition in terms of survival were not measured.

2.4. Inter-specific competition between geese in West Greenland

Todd's Canada Geese, *Branta canadensis interior*, which spend the winter months in the north-east of the United States of America feeding on agricultural land, has recently expanded its breeding range from Baffin Island, into parts of West Greenland (e.g. Bennike, 1990; Frimer & Nielsen, 1990; Boertman, 1994; Fox *et al.*, 1996). Previously, the low tundra of West Greenland was exploited only by Greenland White-fronted Goose, *Anser albifrons flavirostris*, a species which traditionally winters in peat-bogs in the western parts of the British Isles (Salmonsén, 1950, 1967, 1990). In the late 1970s, the Greenland White-fronted Goose was considered threatened. A hunting moratorium in the UK resulted in the population recovering from 10,000 to stabilise at ~35,000 birds in just over a decade (Fox *et al.*, 1994).

Canada Goose colonisation of Greenland has been rapid. For example, in 1992, a team of goose biologists visiting the Isunngua area (67°05'N, 50°30'W) north of Kangerlussuaq, found 12 Canada and 160 White-fronted Geese (Wright & Mitchell, 1993); in 1997, the same team visited the same area and found approximately 200 Canada and 40 White-fronted Geese. Furthermore, only Canada Goose families were observed at some traditional White-fronted Goose breeding sites (Kristiansen, 1998).

Dramatic population increases such as those recorded for the Greenland White-fronted Goose (in winter), and latterly for Canada Geese (in summer), have been described for many goose populations in both Nearctic and Palearctic regions, where formerly, winter-time hunting and associated disturbance acted to control abundance. Hunting restrictions and the widespread use by geese of agricultural land as winter feeding sites are believed to have led to population increases (Madsen, 1987).

Goose biologists now believe that goose population regulation mechanisms occur on the breeding grounds (Ebbinge, 1985, 1991; Madsen *et al.*, 1999). Population regulation may, for example, occur as a consequence of scramble competition for food. Geese are known to spend a lot of time feeding, especially during crucial periods, e.g. during brood-rearing and moult. Faecal analyses have shown that birds generally select for high quality vegetation at these times (Fox *et al.*, 1998), and this is often in short supply in the arctic (e.g. Alisaukas & Ankney, 1992; Afton & Paulus, 1992; Hohman *et al.*, 1992).

Consequently it may be hypothesised that geese breeding in West Greenland compete both intra- and inter-specifically for limited resources. There is evidence that White-fronted and Canada Geese species exploit similar habitat in the tundra landscape of West Greenland, indicating the possibility of inter-specific competition (Wright & Mitchell, 1993; Fox *et al.*, 1996; Kristiansen, 1998). Observations of the interactions between closely related species that are forced to co-exist (e.g. as a result of a recent colonisation event) are rare. However such events do offer unique opportunities for studying the potential for competition and its effects on the inhabitants of natural ecosystems (e.g. Fabricius *et al.*, 1974; Clode & Macdonald, 1995).

Schoener (1983) observed that generally, large species are more likely to out-compete smaller species. The Canada Goose race which is colonising Greenland is between 1.2x (females) and 1.6x (males) heavier than the White-fronted Goose (Palmer, 1976; Cramp & Simmons, 1977; Fox *et al.*, 1996; Jarrett & Warren, 1998), suggesting that if interactions occur, Canada Geese would be the superior competitor. Since West Greenland has hitherto only been exploited by White-fronted Geese (Fox & Stroud, 1988), it may be assumed that this species formerly utilised its fundamental niche. Inter-specific competition, particularly for nest-, brood-rearing and moulting sites, may now be occurring with the result that the White-fronted Goose is forced to 'realise' a narrower niche. The sudden arrival and expansion of the Canada Goose is therefore likely to enhance regulation mechanisms operating on White-fronted Goose populations.

The previous allopatry of the Canada and White-fronted Goose in this region (see Figure 1), may be invoked as Type I evidence for competition. Type II evidence for competition is suggested by the recent population trends of geese in Isunngua (i.e. Canada Geese numbers have increased, while White-front numbers have decreased; see Figure 2). However, these observations combine to indicate only the possibility of competition between the two species. This paper is concerned with identifying and presenting Type III evidence concerning inter-specific competition between the two goose species at the time of moult.

For approximately four weeks, post-breeding geese undergo a simultaneous body and wing feather moult (Owen, 1980). Whilst plumage re-grows, birds are unable to fly and are consequently more susceptible to predation so they tend to graze in close proximity to open water (e.g. Madsen & Mortensen, 1987). Also, since birds' feathers are composed largely of

protein, a nutrient which is of restricted availability to herbivores in the environment (Hohman *et al.* 1992), high quality foods are often selected for. As birds scramble to obtain dietary protein, confinement to the edges of water bodies during the moult has the potential to cause over exploitation of local food resources,. Thus the mechanism for competition between White-fronted and Canada Geese may be expected to involve food selection at the time of moult.

While a few studies on the diet of the Greenland White-fronted Goose have been undertaken on the breeding grounds (Madsen & Fox, 1981), very little is known about the feeding behaviour of Canada Geese in West Greenland (Kristiansen, 1997). If for example, food competition occurs between White-fronted and Canada Geese, the degree of dietary similarity may be expected to be greatest between allopatric populations and smallest between sympatric populations. The extent to which a species alters its diet should reflect which is the dominant species in the interaction, that is, when in competition, the species whose diet shifts least from its ideal diet without competition (Clode & Macdonald, 1995).

Thus the hypothesis to be tested states that Greenland White-fronted Geese shift their diet to include less-nutritious food items when in the presence of Canada Geese. Any apparent niche shifts by geese living in sympatric situations may then indicate the phenomenon of inter-specific competition.

Figure 1: The breeding distribution of White-fronted (green) and Canada Geese (red) in the Nearctic (redrawn from Palmer 1976). The apparent allopatry of White-fronts and medium sized Canada Geese (i.e. *B. c. interior*) may be viewed as Type I of interspecific competition. The recently recorded sympatry in West Greenland is shown as green/red hatching.

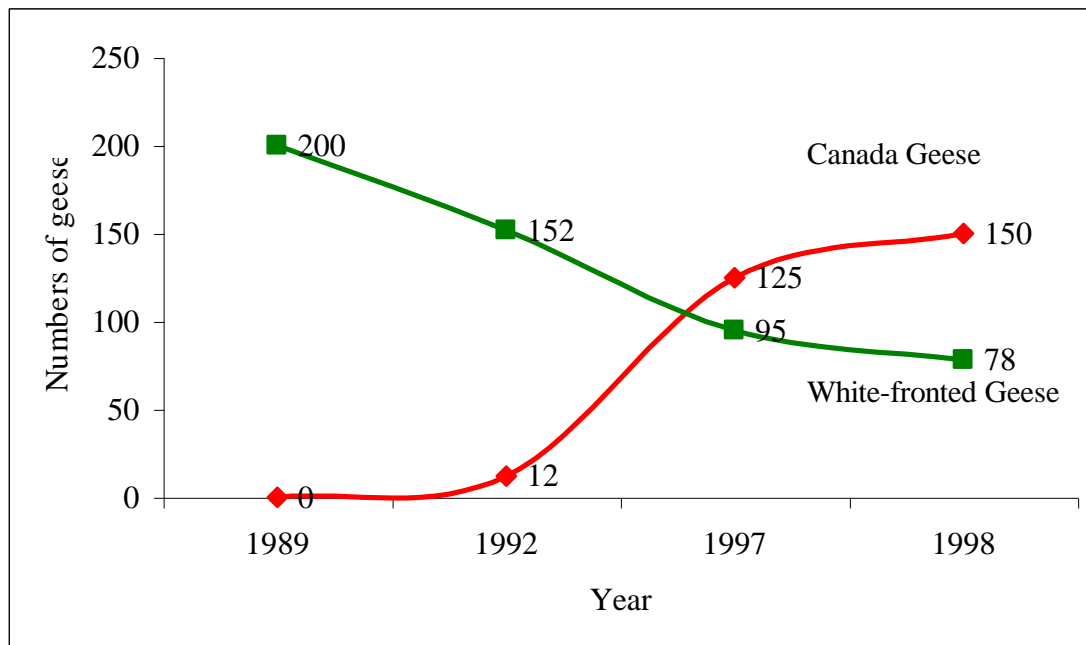


Figure 2: Numbers of White-fronted and Canada Geese in Isunngua, West Greenland: 1989-1998. The inverse population trend represents Type II evidence for competition, with Canada Geese being the superior species.

3. METHODS

Field work was conducted during the period 1-26 July 1998 when non-breeding Greenland White-fronted Geese and Canada Geese were moulting in the Isunngua area, Sisimiut Municipality, of West Greenland (67°05'N, 50°30'W). Isunngua is positioned approximately 60km north of the arctic circle, at the western edge of the Greenland ice-sheet and lies approximately 25km north-east of Kangerlussuaq (Søndre Strømfjord) (Figure 3).

Figure 3: The position of Isunngua in West Greenland

The landscape of Isunngua is one of gently sloping hills (100-600 m above sea level) with numerous pools and lakes in broad valleys separated by whale-back ridges. The region experiences a continental climate with low precipitation, low humidity and high insolation.

Lowland plant communities are dominated by *Calamagrostis* spp. grassland with a variety of herbs such as *Stellaria longipes* and *Cerastium alpinum*. Variations in aspect and drainage result in the replacement of this community by shrub vegetation, with *Salix glauca* flourishing on south-facing slopes and along stream-sides while *Betula nana* and *Ledum palustre* dominate slopes with a more northerly aspect.

Three study sites were chosen (Figure 4):

- 1 A sympatric site where both species of geese co-existed on a 20 ha lake at an altitude of 200 m above sea level. The site was used by 33 non-breeding Canada Geese and 10-23 White-fronted Geese. On a few days, only five White-fronted Geese were present together with the Canada Geese.
- 2 An allopatric site where 12 non-breeding White-fronted Geese used a 3 ha lake at an altitude of 200 m above sea level.
- 3 An allopatric site where 28-non-breeding Canada Geese and two Canada Goose families (two pairs with two and three goslings) used a 40 ha lake at an altitude of 220 m above sea level.

All lakes had at their edges a carpet of moss and were surrounded by steep slopes with vegetation comprising grasses, sedges and hummocks of *B. nana* and *S. glauca*.

Figure 4: The location of sympatric and allopatric goose study sites in Isunngua, West Greenland 1998.

3.1. Habitat use

Habitat utilisation was measured by assessing dropping (faeces) densities in different areas used by feeding geese. Counts of faeces were made along 96 m transect lines laid out perpendicular to the lake shore. At 5 m intervals the number of faeces were recorded in a 4m² area. Additionally, and during activity budget studies (see below), the distance at which birds were feeding from the shore, during bouts of feeding, was recorded in goose lengths. Only one value from each feeding bout was included in the analysis in order that values could be analysed as independent samples.

3.2. Habitat description

The vegetation of the terrestrial habitat types in which birds were recorded was described on the basis of floristics. To relate species frequency (in the goose faeces) with the available food plant species at different feeding sites, the relative frequency of plant species growing in each habitat used by feeding geese was assessed using the pin-point method. A line transect up to 60m in length (i.e. reflecting the maximum distance that geese fed from the water's edge) was positioned perpendicular to the lake shore. At 5 metre intervals a 10 m sub-transect line was positioned perpendicular to the main transect. At 0.1m 'points' along the sub-transect line, plant species were identified and recorded. Often more than one species occurred at the sampling point and hence all were recorded. In this way, vegetation was sampled at 3 positions at the sympatric site and 2 positions at each of the allopatric sites. At 5 m intervals 10 m long sub-transect lines were placed at right angles to the main transect. At 10 cm intervals along these sub-transect lines, plant species were identified and recorded.

3.3. Diet assessment from faecal analysis

Geese digest their food plants inefficiently, excreting the epidermis of ingested vegetation in the faeces. As most plant species have specific epidermal characteristics, a dietary analysis is possible on the basis of microhistological identification of epidermal fragments in the faeces (Owen, 1975).

In order to assess diet, fresh faecal pellets from at least 10 different individual geese (of each species) and reference plant material were collected from each site. Collections were made at the end of activity budget fieldwork to avoid disturbing geese during the intensive observation period (see below). At the sympatric site faeces of both species were collected when exact species positions were separate. All droppings were sun-dried and stored separately in paper bags for later laboratory analysis.

To identify the plant fragments in faeces, reference plant specimens were collected from each site and flat dried in a press for transportation. In the laboratory, one cutinised epidermis (approximately 1cm²) of different plant parts (i.e. lower leaf, upper leaf and stem) was carefully retrieved under a binocular microscope. A plant part was soaked for 24 hours in soapy water, then deposited on a binocular slide in a drop of household bleach. The soapy water softened the dried tissues, and the bleach served to clear the pigments. An epidermal fragment was then cleaned by scraping away the opposite epidermis and inside tissues with a scalpel. The cleaned epidermis was washed in water, then mounted outside up on a microscope slide in glycerine for permanent storage and future reference. Several photographs of different plant parts from each species were taken under the microscope at

200-400x magnification (see plates in Appendix 1 for examples of photographic material collected).

Diet was assessed for 10 different geese of each species in each situation (i.e. the allopatric and sympatric situations). Prior to examination, faeces from each goose were separately mixed in a 75% alcohol until the sample had a thick but fluid consistency. A sub-sample from each 'faecal solution' was removed with tweezers. Sub-samples were spread on separate microscope slides so that they covered approximately a 22 x 40mm cover-slip when mounted in glycerine. Generally, a fragment cover of about 50% was achieved without excessive overlapping.

To assess the area of epidermis of each plant species, sampling was undertaken using a point quadrat approach. If fragments overlapped at the sampling point, only the uppermost fragment was identified and recorded. Points were examined every 5 mm along four transects per sub-sample. Sufficient sub-samples from each faeces were examined to provide approximately 100 presence records. Plant fragments in faeces were identified to generic level where possible, but subsequently pooled in to the following main taxonomic groups: mosses (Bryophyta), *Equisetum* spp. (Equisetaceae), Dicotyledones, grasses (Poaceae) and sedges (Cyperaceae).

3.4. Diet selectivity

Based on the pin-point results from the faecal analysis, percentage occurrence of the main food plant groups was estimated. In order to investigate diet selectivity, Manly's alpha preference index (Krebs, 1989) was calculated for each of the taxonomic plant groups for all situations in which both goose species were observed, viz.:

$$\alpha_i = r_i / n_i \cdot 1 / \sum(r_j / n_j)$$

Where:

- α_i = Manly's alpha (preference index) for prey type i
- r_i, r_j = Proportion of prey type i or j in the diet (i and $j = 1, 2, 3, \dots, m$; where m is the number of prey types possible)
- n_i, n_j = Proportion of prey type i or j in the environment

When there is no selective feeding occurring $\alpha_i = 1/m$, but when $\alpha_i > 1/m$ then prey i is preferred in the diet and when $\alpha_i < 1/m$, prey species i is avoided.

3.5. Niche breadth

Standardised niche breadth (ranging from 0-1) for the diet was measured using Levins' formula (Krebs, 1989), viz.:

$$B_A = (1 / \sum p_i^2) - 1 / n - 1$$

Where:

- B_A = Levin's standardised niche breadth
 p_i^2 = The relative proportions of each prey item in the diet
 n = Total number of prey types

3.6. Niche overlap

In comparisons of allopatric versus sympatric situations, niche overlap in the diet was calculated using Pianka's adaptation of MacArthur & Levins' formula (Krebs, 1989), viz.:

$$O_{jk} = \sum_n p_{ij} p_{ik} / \sqrt{\sum p_{ij}^2 \sum p_{ik}^2}$$

Where:

- O_{jk} = Pianka's measure of niche overlap between species j and species k
 p_{ij} = Proportion resource i is of the total resources used by species j
 p_{ik} = Proportion resource i is of the total resources used by species k

The measure of niche overlap ranges from 0 (no shared resources) to 1 (complete overlap).

3.7. Activity budgets

The diurnal activity of sympatric and allopatric goose flocks was observed and recorded from using 20-60x magnification telescopes from concealed positions (camouflage hides) on high ground.. Observation positions afforded unrestricted views over the goose moulting/feeding sites. Birds' activity was recorded using two methods, concurrently:

1. At 5-minute intervals the flock was scanned and the position (habitat type) and the activity of all geese present on land or water was noted (after Altman, 1974). Birds' position was allocated to 5 habitat types and activity was assigned to the following categories: feed, head-up, preen, swim, walk, wing-flap, wing-stretch, up-end (in water) head submerged (feeding on submerged vegetation), aggression, sleep, drink.
2. In the intervals between monitoring activities, individual birds' distance from the water's edge was estimated (in goose lengths) and all goose-goose interactions were recorded.

Observation bouts ranged 3-6 hours and were dispersed over the day and night so that full 24-hour watches were made at all sites.

4. RESULTS

4.1. Habitat use

Observations on the distribution of feeding geese and dropping counts at the sympatric site (Figure 5a) showed that birds rarely grazed beyond 50 m distance from the shore. White-fronted Geese grazed significantly closer to the shore (mean maximum distance: 13.8 ± 3.00 goose lengths) than Canada Geese (mean maximum distance: 40.6 ± 7.61 goose lengths) ($t = 3.391$, $df = 14$; $p < 0.001$).

Observations together with dropping counts made at the allopatric White-fronted Goose (Figure 5b) and allopatric Canada Goose sites (Figure 5c) also revealed that birds rarely exploited areas greater than 50 m from the shore. White-fronted Geese were recorded feeding to a mean maximum distance of 65.0 ± 9.57 goose lengths ($n = 10$) from the shore, while allopatric Canada Geese grazed to a mean maximum distance of 26.3 ± 3.90 goose lengths ($n = 12$) from the shores of their respective moulting lakes. High densities of droppings within 10m of the shore do not necessarily reflect high grazing intensity, but rather the use of this zone as a roosting area.

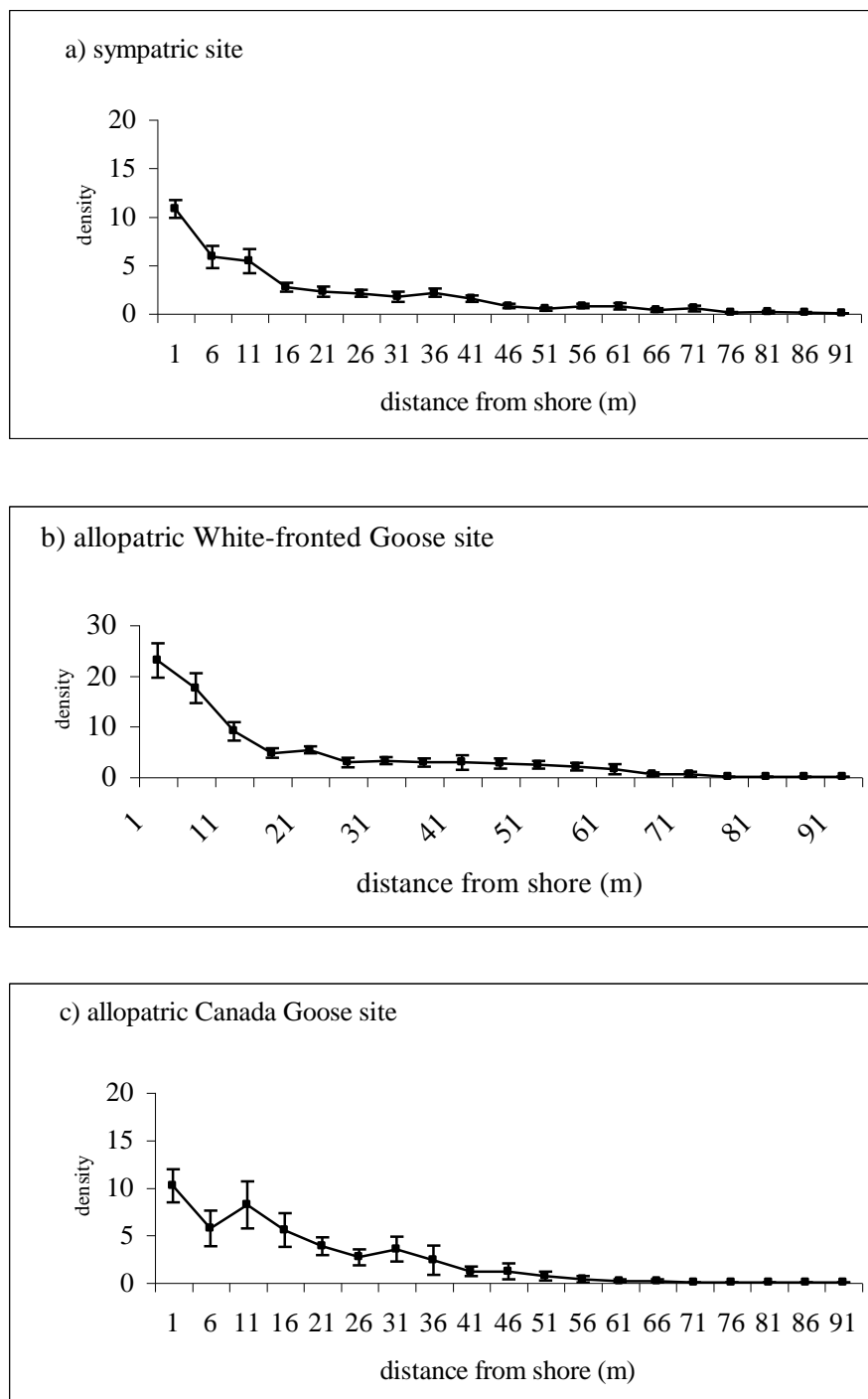


Figure 5: Mean (+/- 1SE) dropping densities recorded at the three sites: a) the sympatric site; b) the allopatric White-fronted Goose site 3 line transects; c) the allopatric Canada Goose site. Droppings were counted in a 3.1m² area, at 5m intervals along 3 line transects positioned to a distance of 91 m perpendicular from the lake edge.

4.2. Habitat description

The relative frequency of the main plant groups, recorded in 15m transects at 5 m intervals and between 1-56 m of the shoreline, are shown in Figure 6a for the sympatric site.

Generally, and within 5 m of the shore, bryophytes dominated with Dicotyledones and Poaceae species providing most cover at distances beyond. Cyperaceae species reached their highest representation (14% cover) in the 6-11m band, and did not exceed >10% cover elsewhere. Overall cover by Poaceae species exceeded 50% at distances greater than 41m from the shore, with *Equisetum* species also becoming more prominent towards the outer edge of the feeding zone.

The relative frequency of the main plant groups, recorded in 15m transects at 5 m intervals and between 1-56 m of the shoreline, are shown in Figure 6b for the allopatric White-fronted Goose. Overall, Cyperaceae was the dominant plant group. Although Cyperaceae appeared to have negligible representation at approximately 6 m from the shore, species in this group ranged 38-62 % cover at distances of up to 45 m from the water edges. Bryophytes were also plentiful and accounted for around 30% cover within 6 m, and 20-25% cover within a band 11-26 m of the shore. Where a soligenous flush occurred at 31 m, bryophytes peaked at approximately 44% cover declining rapidly on the drier ground at greater distances.

Dicotyledonous species fluctuated in cover abundance. Generally this group had low abundance near to the shore but increased to up to 30% on ground away from open water. Poaceae also showed a fluctuating pattern of cover but generally increased in cover away from the shore. Interestingly, at 6 m from the shore, grass species accounted for almost 58% cover and appeared to replace sedges (which were dominant in flanking zones). Equisetaceae only appeared at very low abundance in the plant communities at 46 m.

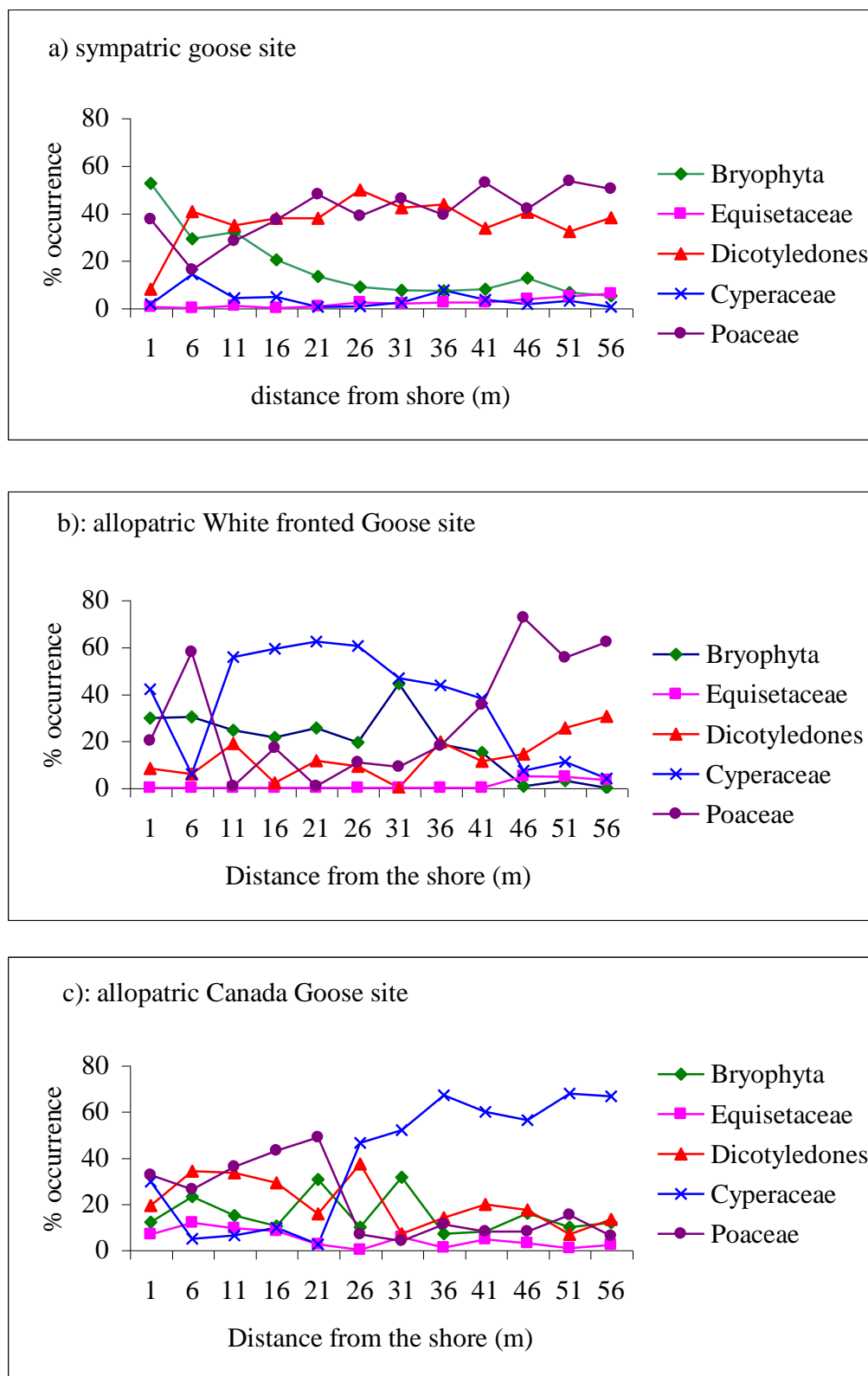


Figure 6: The vegetation gradient at the three sites: a) the sympatric site; b) the allopatric White-fronted Goose site; c) the allopatric Canada Goose site. Vegetation was recorded along 3 line transects positioned 56m perpendicular from the lake edge.

The relative frequency of the main plant groups, recorded in 15m transects at 5 m intervals and between 1-56 m of the shoreline, are shown in Figure 6c for the allopatric Canada Goose site. At this site, Bryophyta were most dominant (up to 32% cover) in the zones within 30 m of the shore. A rather similar pattern of abundance was shown by Poaceae species: cover peaked at 49% at 21 m, falling to between 4-11% cover at greater distances. Cyperaceae species had lowest cover where previously mentioned groups were most dominant: peak dominance was recorded at 68% cover at 51 m from the shore. Equisetales were recorded at uniform but low abundance (between 3-12%) up to distances of 16m from the shore, and had negligible cover at greater distances. Dicotyledones were more abundant at this site than at the White-front and sympatric sites, providing approximately 30% cover at distances up to 26m from the shore and around 20% at greater distances.

Figure 7 summarises the overall percentage cover of the main plant groups within the goose feeding areas up to 56 m distant from the shore at each site. Bryophytes were fairly uniformly represented at 15-20%, while Equisetaceae, at <5% cover were scarce at all three sites. Dicotyledones were most prominent at the sympatric site (37% cover) and least prominent at the allopatric White-fronted Goose site (13% cover). The most obvious difference between the sites was with respect to the percentage cover by Cyperaceae species. This plant group was dominant at the allopatric sites with approximately 30-35% cover but very scarce at 3.7% cover at the sympatric site. By far the most important plant group in terms of cover was the Poaceae: over 40% cover at the sympatric site and over 20% and 30% cover at the allopatric White-fronted and Canada Goose site respectively.

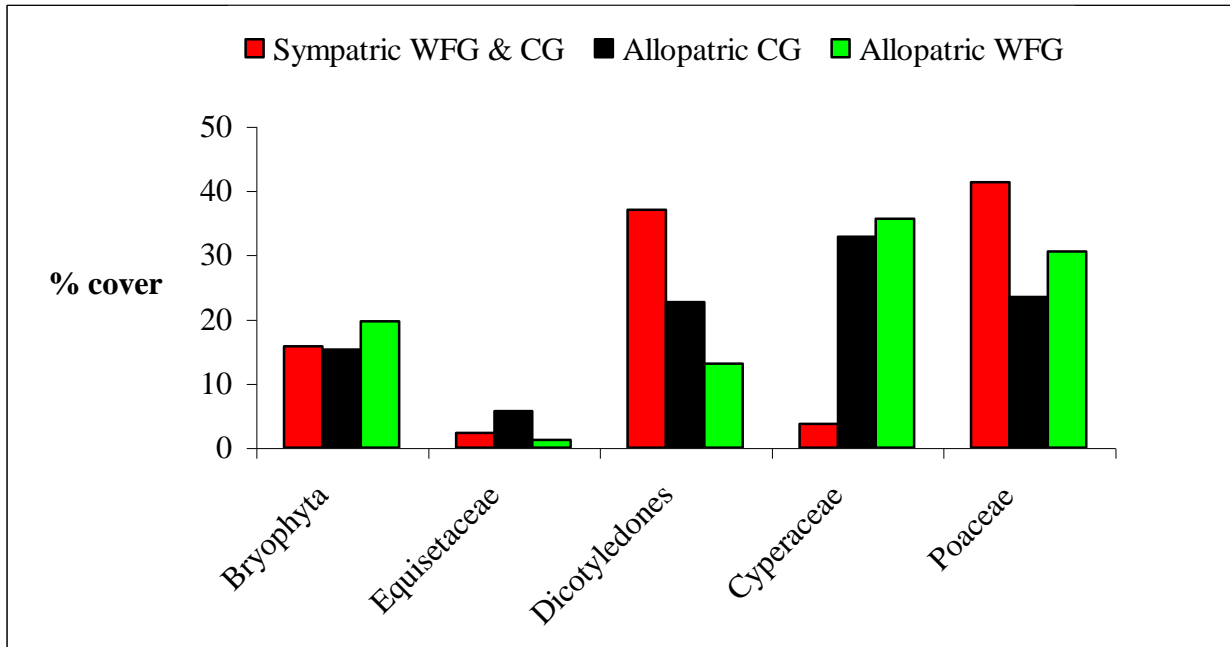


Figure 7: Overall percentage cover of the plant groups in the goose grazing areas at the three sites. WFG: White-fronted Goose; CG: Canada Goose.

4.3. Diet assessment from faecal analysis

Table 1 summarises the representation of each plant group in the diet of allopatric and sympatric geese.

Table 1: Percentage representation of plant groups in the diet of allopatric and sympatric geese

Plant Group	% Representation in Diet			
	White-fronted Geese		Canada Geese	
	Sympatric (<i>n</i> = 10)	Allopatric (<i>n</i> = 10)	Allopatric (<i>n</i> = 10)	Sympatric (<i>n</i> = 10)
Bryophyta				
Mean ± SE	20.0 ± 2.96	3.9 ± 0.62	3.0 ± 0.84	2.4 ± 0.43
range	8-32	1-7	0-10	1-5
Equisetaceae				
Mean ± SE	7.6 ± 1.35	1.7 ± 0.63	12.7 ± 1.25	21.0 ± 1.85
range	3-14	0-6	8-19	11-30
Dicotyledones				
Mean ± SE	2.3 ± 0.42	0.9 ± 0.28	2.1 ± 0.36	2.0 ± 0.45
range	1-5	0-2	0-4	0-4
Cyperaceae				
Mean ± SE	27.0 ± 2.24	68.5 ± 2.21	31.5 ± 2.49	24.2 ± 1.53
range	19-40	57-79	19-48	15-33
Poaceae				
Mean ± SE	42.0 ± 3.58	23.3 ± 1.51	49.4 ± 2.47	48.8 ± 1.54
range	23-56	18-33	33-57	42-56
Unknown				
Mean ± SE	1.2 ± 0.65	1.7 ± 0.47	1.3 ± 0.39	1.6 ± 0.72
range	0-6	0-4	0-4	0-6

In sympatry, the diet of both species comprised mainly Poaceae (White-fronts: 42.0% \pm 3.58; Canada Geese 48.4% \pm 1.54) and Cyperaceae (White-fronts: 27.0% \pm 2.24; Canada 24.2% \pm 1.53). Dicotyledons were poorly represented in the diets of birds in all situations (on average, *circa* 2%). Equisetaceae were eaten by both species, but more so by Canada Geese (12.7 \pm 1.25 in allopatry; 21.0 \pm 1.85 in sympatry). White-fronts in sympatry with Canada Geese, ingested more bryophytes (20.0 % \pm 2.96) than birds in allopatry (3.9 % \pm 0.62). On average, the diet of Canada Geese comprised approximately 3% bryophytes.

The variation in birds' diet at each site was investigated further using Principal Components Analysis. Table 2 shows the correlation matrix obtained.

Table 2: PCA of proportional contributions of different vegetation types in faeces collected from White-fronted and Canada Geese occurring in sympatry and allopatry

Eigenvalue	2.7657	1.3342	0.6451	0.2509	0.0042
Proportion	0.553	0.267	0.129	0.050	0.001
Cumulative	0.553	0.820	0.949	0.999	1.000

Component loadings

Variable	PC1	PC2	PC3	PC4	PC5
Equisetaceae	-0.521	-0.269	-0.142	0.742	-0.291
Poaceae	-0.566	-0.071	-0.079	-0.638	-0.511
Cyperaceae	0.563	-0.222	0.285	0.081	-0.739
Dicotyledones	-0.274	0.546	0.779	0.132	-0.058
Bryophyta	0.124	0.759	-0.534	0.133	-0.325

The PC 1 and PC 2 axis scores of the ordination explained 82% of the variation in the individually sampled faeces. They are plotted against each other in Figure 8. With respect to the PC 1 axis, scores for the faeces from allopatric White-fronted Geese cluster to the right of the plot. Consideration of the individual component loadings indicates that this end of the axis represents high proportions of Cyperaceae. This clustering effect illustrates the high proportion of Cyperaceae in the diet of allopatric White-fronts. The scores for the faeces of sympatric White-fronted Geese occupy a larger area of the plot signalling the greater range of plant groups eaten. Those birds with faeces containing relatively large amounts of bryophytes are separable with high PC 2 axis scores. Faeces from allopatric and sympatric Canada Geese had low PC 1 axis scores reflecting the high ingestion of Poaceae and Cyperaceae and low ingestion of Bryophyta. Consequently, the plotted axes scores for allopatric and sympatric Canada Geese show some overlap.

Figure 8

The variation in PC scores of geese in allopatry and sympatry was investigated using ANOVA. There were significant differences between PC scores indicating that allopatric and sympatric birds had different diets. The diet of allopatric White-fronted Geese, as summarised by PC 1, differed very significantly from the diet of sympatric White-fronts and allopatric and sympatric Canada Geese (One-way ANOVA, $F_{3,36} = 47.32$; $p < 0.001$; Tukey's Multiple Comparison Test and see Figure 9a). The diet of sympatric White-fronted Geese, as summarised by PC 2, differed very significantly from the diet of allopatric White-fronts and sympatric Canada Geese (One-way ANOVA, $F_{3,36} = 17.56$; $p < 0.001$; Tukey's Multiple Comparison Test and see Figure 9b).

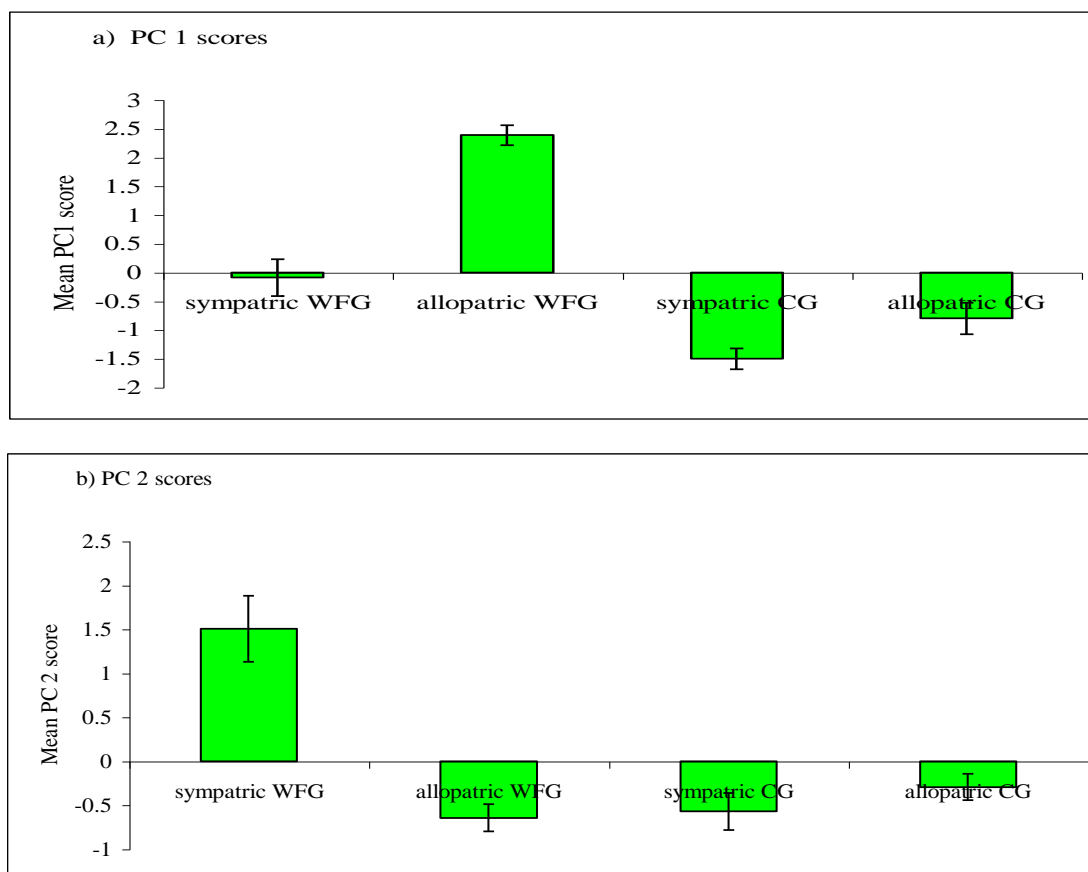


Figure 9: Mean ± 1 SE PC scores for the diet (assessed by faecal analyses) of geese at allopatric and sympatric sites: a) PC 1; b) PC 2.

4.4. Diet selectivity

Figures 10 and 11 compare the diet of geese (assessed by faecal analysis) with the availability of plant groups at the sympatric and allopatric sites respectively. Apparent preferences of each goose species for each plant group are indicated by Manly's Preference Indices.

In sympatry (Figure 10a & 10b) neither goose species selected actively for Poaceae, but both showed a high preference for Cyperaceae. Dicotyledons were clearly avoided. Canada Geese selected highly for Equisetaceae, but White-fronts showed only a minor preference for this group. Although White-fronted Geese did not actively forage for Bryophyta, neither did they avoid plants in this group. In comparison, Canada Geese appeared to avoid bryophytes.

In allopatry the preferred food plants of White-fronted Geese (Figure 11a) were Poaceae and Cyperaceae, the latter being most strongly selected. White-fronts also appeared to actively forage for Equisetaceae although the content in the diet was negligible. Dicotyledons and Bryophyta were avoided. The allopatric Canada Geese (Figure 11b) showed a strong preference for Equisetaceae, followed by Poaceae. Cyperaceae species were also selected while Dicotyledones and Bryophyta appeared to be of no importance in the diet and were avoided.

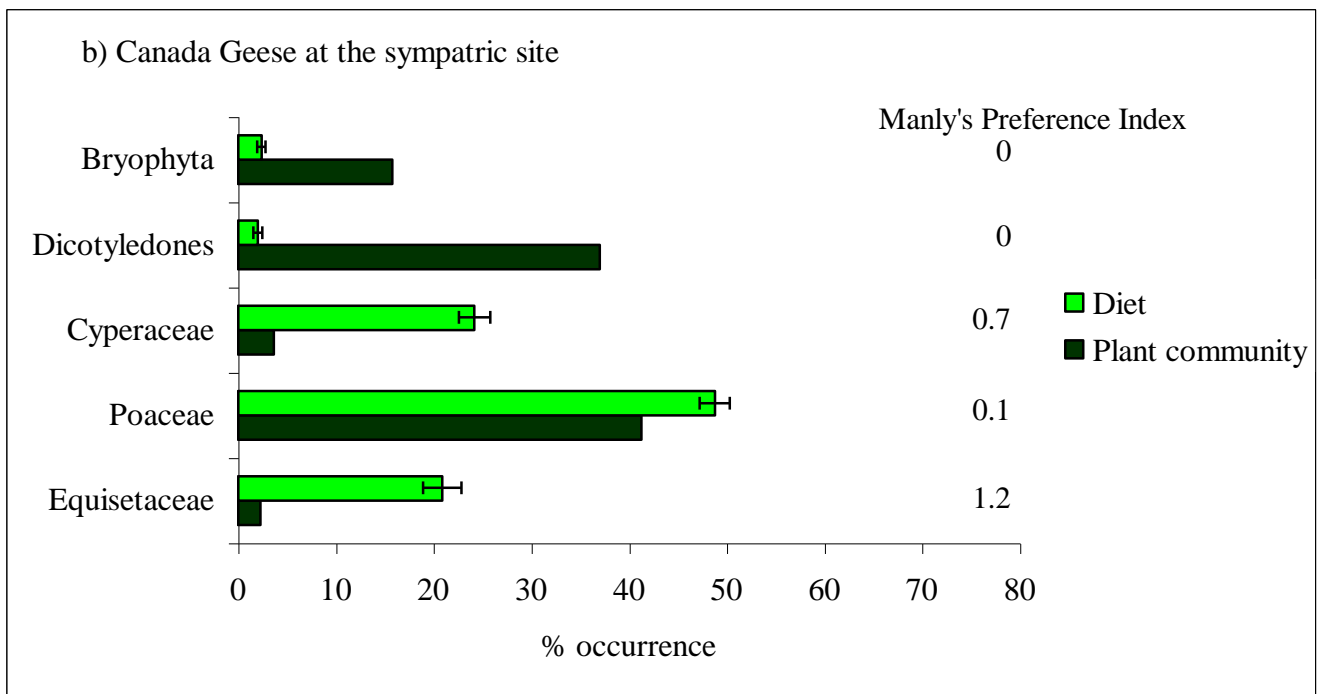
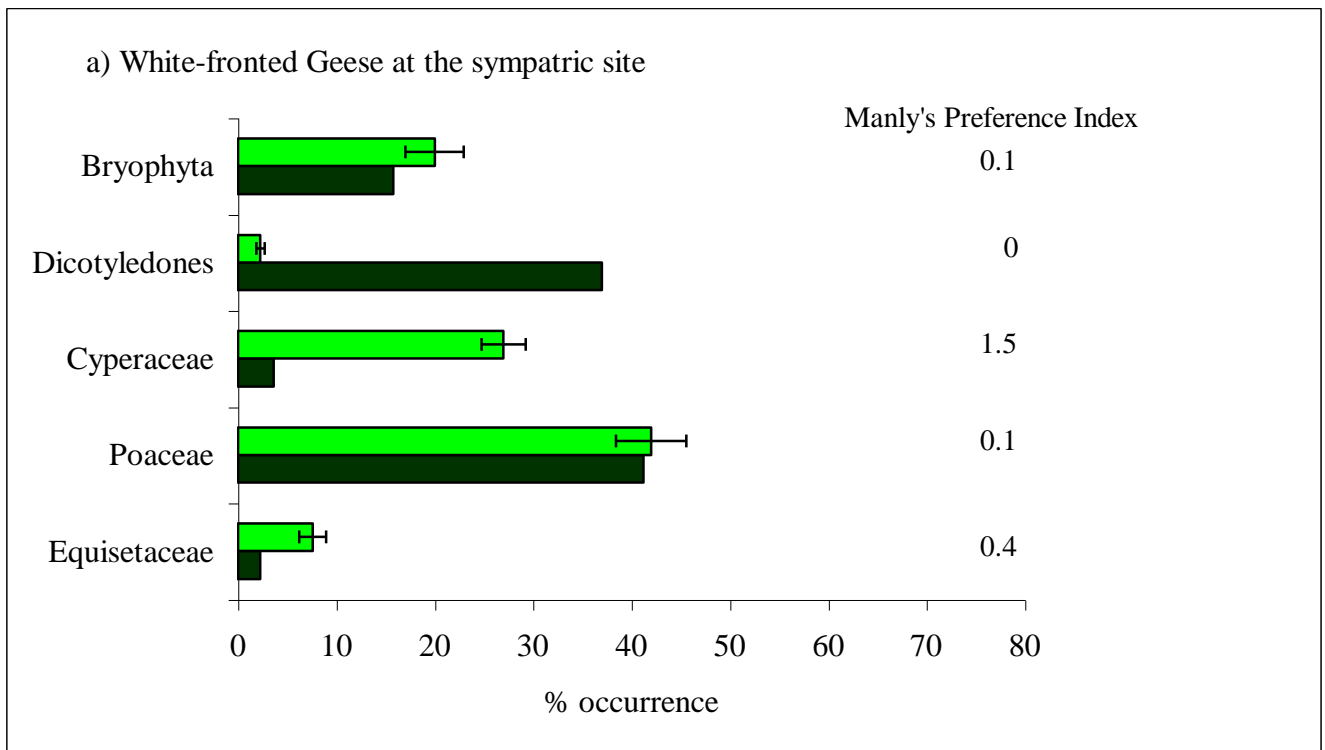


Figure 10: Percentage occurrence (mean \pm 1SE) of plant types in diet of geese: a) in diet of White-fronted Geese and in the plant community at the sympatric site; b) in the diet of Canada Geese and in the plant community at the allopatric site. Manly's preference indices (α) are given: if $\alpha < 0.2$, the plant group is not preferred food; if $\alpha > 0.2$, the plant group is preferred food.

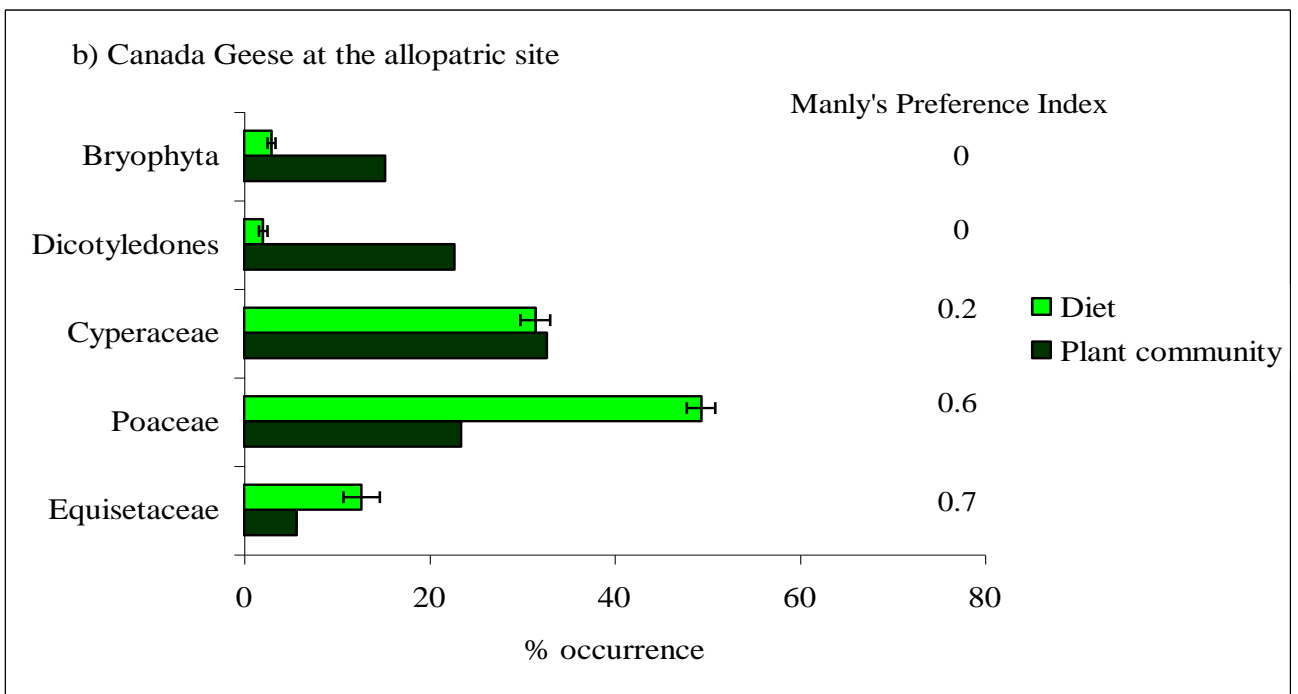
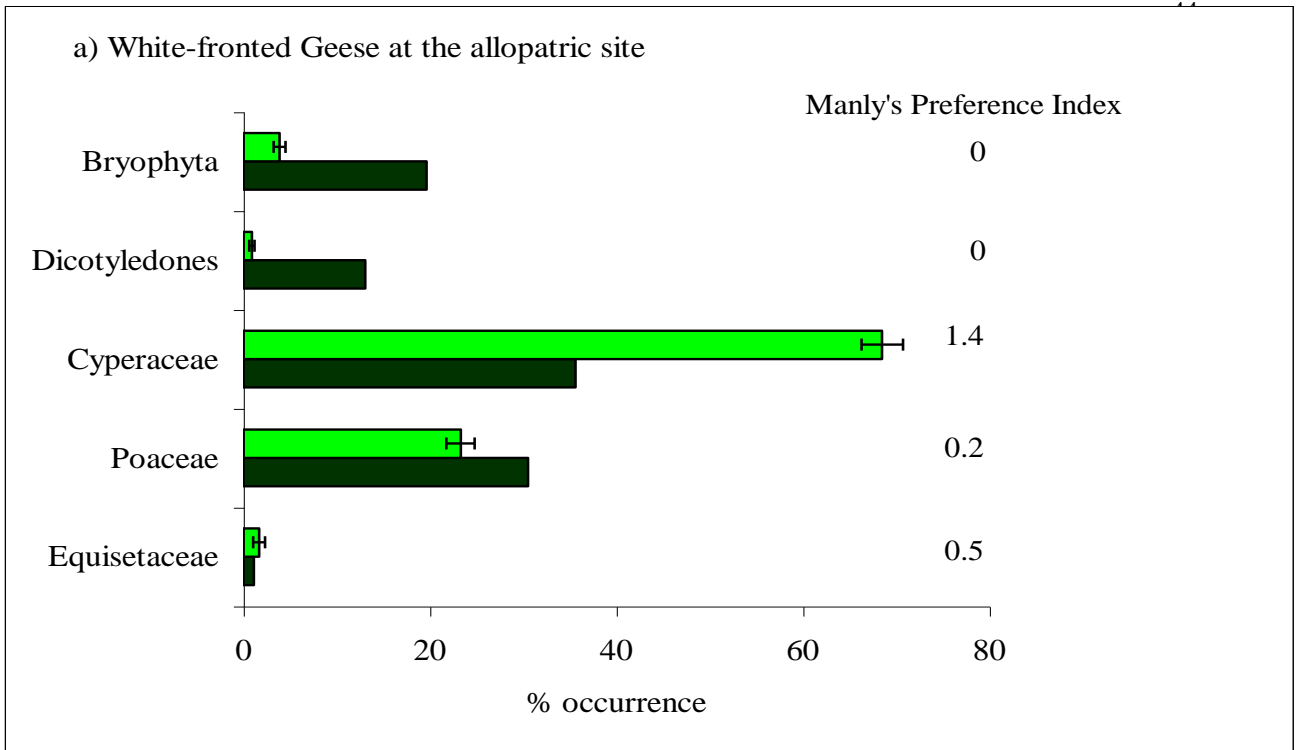


Figure 11: Percentage occurrence (mean \pm 1SE) of plant types in diet of geese: a) in diet of White-fronted Geese and in the plant community at the sympatric site; b) in the diet of Canada Geese and in the plant community at the allopatric site. Manly's preference indices (α) are given: if $\alpha < 0.2$, the plant group is not preferred food; if $\alpha > 0.2$, the plant group is preferred food.

4.5. Niche breadth

Mean and median niche breadth of the two species in sympatry and allopatry are presented in Table 3. In the sympatric situation both goose species showed relatively broad diets, with White-fronts having a broader diet than Canada Geese. While Canada Geese increased their niche breadth (from a median of 0.42 to 0.48) in the presence of White-fronted Geese, this difference was not significant (Mann-Witney U Test; $W = 84.0$; $n = 10$; *n.s.*). White-fronted Geese also increased their niche breadth (from a median of 0.23 to 0.55) when in sympatry with Canada Geese and this difference was very significant (Mann-Witney U Test; $W = 55.0$; $n = 10$; $p < 0.001$).

Table 3: Mean ($\pm 1SE$), median and range of niche breadth shown by White-fronted and Canada Geese at the sympatric and allopatric sites in Isunngua, West Greenland

	Sympatric Site		Allopatric Site	
	White-fronted Goose $n = 10$	Canada Goose $n = 10$	White-fronted Goose $n = 10$	Canada Goose $n = 10$
Mean Niche Breadth	0.54 \pm 0.023	0.47 \pm 0.017	0.23 \pm 0.019	0.43 \pm 0.019
Median Niche Breadth	0.55	0.48	0.23	0.42
Range	0.41-0.64	0.41-0.56	0.13-0.33	0.35-0.55

4.6. Niche overlap

The similarity in diet between the two goose species is shown by niche overlap indices given in Table 4. When together the two species used very similar food plants demonstrated by a niche overlap score of 0.92. While it is apparent that Canada Geese use nearly identical resources in allopatry and in sympatry (overlap score of 0.98), White-fronted Geese show less similarity of diet between the states of allopatry or sympatry (niche overlap score of 0.74).

Table 4: Comparisons of niche overlap indices for the two species at the sympatric and allopatric sites; WFG: White-fronted Goose; CG: Canada Goose.

	Sympatric WFG & Sympatric CG	Sympatric WFG & Allopatric WFG	Sympatric CG & Allopatric CG
Niche Overlap	0.92	0.74	0.98

4.7. Activity budgets

A total of 131 scanning hours (scanning every 5 minutes) were obtained: 69 hours at the sympatric site, 33 hours at the allopatric Canada Goose site and 31 hours at the allopatric White-fronted Goose site. Sympatric geese spent between 36 and 38% of the day grazing. White-fronts in sympatry and allopatry spent slightly more time resting than Canada Geese. Allopatric White-fronted Geese also spent much more time preening and were apparently more frequently vigilant than either species in sympatry. Interactions between the two species were recorded on 45 occasions. In every case Canada Geese were superior, forcing White-fronts to retreat even when they were outnumbered (which occurred on 21 occasions). All aggressive interactions involved birds grazing on land, never when birds were swimming on water.

5. DISCUSSION

During the post breeding moult period, arctic geese are rendered flightless. Until wing feathers are re-grown, they are susceptible to attack by mammalian ground predators, such as Arctic Foxes, *Alopex lagopus* (Madsen *et al.*, 1992). Flocks of geese therefore feed in close proximity to the shores of lakes, actively taking refuge on open water as a response to phantom or potential predators (Madsen & Mortensen, 1987; Fox *et al.*, 1995). Consequently, this confinement of birds to narrow zones adjacent open water has the potential to cause overexploitation of local food resources. At this time birds are feeding in order to meet demands for protein required to replace moulted feathers (Fox *et al.*, 1998), and to accumulate fat reserves to fuel autumn migration to wintering areas (Owen & Black, 1989).

In Isunngua, moulting White-fronted and Canada Geese, rarely foraged for food resources growing at distances greater than 50 m from open water. Within these narrow zones, birds foraged in habitats where potential food plants showed varying degrees of availability at the three study sites. Despite differences in plant availability between sites, faecal analyses revealed that both goose species had dietary preferences for Cyperaceae, Poaceae and Equisetaceae species. These plants were frequently selected above their levels of occurrence in the community, refuting the claim of Hohman *et al.* (1992) that wildfowl only select foods in proportion to their availability. These preferred plant groups are known to contain comparatively high crude protein levels (J. N. Kristiansen unpublished data; see Table 5), suggesting that geese moulting in Isunngua actively forage for the most proteinaceous plant species.

Table 5: Crude protein content: Percentage dry weight (mean \pm se) of main food plants for White-fronted Geese and Canada Geese (specimens collected in Isunngua, West Greenland 1998. ANOVA (log transformed values) was used to test for differences in protein content. Similar lower case letters indicate no significant differences between mean values based on Tukey Multiple Comparisons test ($p < 0.005$) (data provided by J. N. Kristiansen).

	Bryophyta	<i>Equisetum arvense</i>	<i>Eriophorum scheuchzeri</i>	<i>Carex rariflora</i>	<i>Poa arctica</i>
Crude Protein (% dry weight)	11.67 \pm 0.24 ^a	20.15 \pm 0.30 ^b	18.14 \pm 0.08 ^c	20.16 \pm 0.11 ^b	23.09 \pm 0.11 ^d

Faecal analyses from the sympatric site revealed that Canada Geese select most strongly for Equisetaceae. Overall, this species ingested greater amounts of high protein food plants than White-fronted Geese. Although the faeces of sympatric White-fronted Geese contained greater amounts of Cyperaceae than did the faeces of sympatric Canada Geese, analyses revealed that these geese also ingested large quantities of Bryophyta, more so than when in allopatry. Earlier studies have indicated that Bryophyta comprise low levels of protein, (Madsen & Mortensen, 1987; and see Table 5) and are not the preferred food plants of geese moulting in Greenland (Madsen, 1981; Kristiansen, 1997). Thus, we may infer that when in the presence of Canada Geese, White-fronts show a niche shift resulting in the ingestion of less nutritious food plants.

Faecal analyses showed Canada Geese utilised a broad niche and that their diet changed least in the presence of the other species, suggesting that the new arrival is the dominant competitor. This observation meets theoretical expectations, given larger competitors are more likely to be successful over smaller competitors (Schoener, 1983) and that body mass ratio of male Canada Geese to male White-fronted Geese is approximately 1.6 (Jarrett and

Warren, 1998). Evidently, Canada Geese are generalist grazers, inasmuch as they have comparatively high niche breadth scores. The catholic diet of this species, coupled with large body size may account for the recent success of this goose as a coloniser of West Greenland.

In contrast, allopatric White-fronted Geese showed very narrow niche breadth scores, suggesting that this species is a specialist grazer, selecting for Cyperaceae species in particular. This extreme selectivity for Cyperaceae has been observed in White-fronted Geese spring staging in Iceland (Fox *et al.*, 1998; Kristiansen *et al.*, 1998). Further support for the Cyperaceae grazing trait is presented in Table 6. A faecal analysis study conducted at eight different sites *circa* 70km north of the Isunngua in 1979 (Madsen, 1981), revealed that birds took mainly Cyperaceae species, and had niche breadth scores even more narrow than demonstrated by birds in this study.

Table 6: Percentage frequency of food plants in the diet and mean niche breadth of allopatric non-breeding Greenland White-fronted Geese in Eqaalummiut Nunaat, West Greenland, 1979 (data from Madsen, 1981)

Date	Bryophyta	Equisetales	Dicotyledones	Cyperaceae	Poaceae	Niche Breadth
5/7	0	1	1	94	5	0.06
5/7	0	0	0	98	2	0.01
5/7	1	0	0	96	3	0.02
5/7	0	0	0	99	1	0.01
5/7	0	2	0	97	1	0.02
5/7	0	0	0	95	5	0.03
7/7	3	18	1	64	14	0.29
11/7	2	0	0	90	8	0.11

Sympatric White-fronts showed much higher niche breadth scores than birds in allopatry reflecting the greater variety of plant groups ingested. In effect, White-fronts co-existing with Canada Geese switched to a more generalised diet, possibly as a response to food competition. The ability of White-fronted Geese to take a wider range of plant species suggests that in the absence of Canada Geese, this species has under-exploited many potential food plants growing in lakeside grazing zones. Perhaps, until now, the absence of competitors has allowed the species to evolve forage for the highest quality food plants only.

Canada Geese in allopatry and in sympatry used nearly identical resources (reflected by a high niche overlap score). Nevertheless, Canada Geese were not entirely unaffected by White-fronted Geese. In the presence of White-fronts, the niche breadth of Canada Geese increased slightly, suggesting that these birds also 'scramble' for food resources. In such circumstances of sympatry, where dietary competition cannot be avoided, a shift along at least one dimension of the niche may be expected (Clode & MacDonald, 1995). Indeed the pattern of dietary change shown by co-existing White-fronted and Canada Geese appeared to occur along a spatial dimension. Although individuals of both species foraged in the same 50m zone close to open water, Canada Geese appeared to exploit Poaceae and Equisetaceae species growing at greater distances from the shore, whereas White-fronts remained closer to the edge of the lake, where bryophyte species were dominant.

This type of spatial segregation may be explained in terms of differences in species' wariness to predators. However, at the allopatric site, White-fronted Geese were recorded feeding at greater distances from open water than geese in other situations. It is perhaps more likely that the two species were segregating in order to avoid competition. Although food competition is generally regarded as an example of exploitative or indirect competition, where a joint

resource is being used, Schoener (1983) notes that interference or direct competition may also occur. The mechanism for segregation was clearly observed in terms of aggression interactions. Direct physical confrontations between the two goose species were recorded on 45 occasions, and always when birds were actively feeding together. In every case, and even when outnumbered, Canada Geese were superior to White-fronted Geese. Most encounters involved Canada Geese chasing White-fronts usually because they had approached, while grazing, within 1.5 metres. Consequently White-fronts were very nervous of Canada Geese and would stop feeding and show alert behaviour whenever the other species was nearer than approximately 3 metres (personal observation).

Non-breeding moulting White-fronted Geese are known to select lake systems with expansive lake side grazing areas (Stroud, 1981; Fox *et al.*, 1983). Non-breeding moulting Canada Geese also appear to select the same type of wetland habitat exactly. Since White-fronted Geese simultaneously moult all flight feathers slightly earlier than Canada Geese (Jarrett & Warren, 1997), they may be unable to avoid sympatry with late moulting Canada Geese. This study would suggest that White-fronts forced to moult in sympatry may be subjected to exploitative competition as favoured plant foods are grazed, and interference competition as the more dominant species prevented the smaller species from accessing potential grazing zones.

Studies of tundra vegetation have shown that regular cropping and fertilisation by geese can maintain and increase the quantity and quality of food provided by the sward over short periods in spring and summer (Ydenberg & Prins, 1981; Cargill & Jefferies, 1984; Bazely & Jefferies, 1985). Prop & Deerenberg (1991) demonstrated that the energetic profitability of different plants was governed to a large extent by their size and that birds could modify

intake rates by differences in bite size. Therefore, in terms of offering a growing and renewable resource, grazed plant species growing next to open water refuges may represent an abundant source of protein. Perhaps the arrival of Canada Geese at moult sites in West Greenland may improve the extent of high quality forage available to White-fronted Geese.

In conclusion, the results suggest that inter-specific competition (exploitation and interference) does occur between White-fronted Geese and Canada Geese. However, this study provides a 'snap shot' assessment only: dietary preferences were deduced from faeces collected on one occasion only. Clearly additional and more precise data about diet and microhabitat is required from more sites. Only then will the nature and extent of competitive interactions between the two species become known. Future studies investigating the effects of competition on birds' survival, a true measure of competition, will be particularly challenging, but not impossible. Given that birds can be captured during the period of wing moult, it should be possible to measure body condition and to analyse this with respect to dietary intake (e.g. Owen & Black 1989).

Sustained studies may reveal that the present situation, characterised by the two species overlapping in range and resources use, is a temporary phenomenon. For example, the competitive exclusion of the inferior species (White-fronts) from preferred habitats, may result in it changing its use of alternative resources. The result may then be that White-fronts are able to avoid competition with Canada Geese in the near future. Alternatively, the two species may be able to co-exist, albeit with White-fronts at a lower population size.

However, until further research is carried out, and given that goose population regulation mechanisms are expected to operate on the breeding grounds (Ebbinge, 1985; Madsen, 1987),

perhaps the British Government should continue to provide legal protection to Greenland White-fronted Geese wintering in the UK.

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APPENDIX ONE

PLATES

Photomicrographs (200x magnification) of epidermal surfaces of some major goose food plants accompanied by photos of epidermal surfaces in faeces.

All plant and faecal material collected in Isunngua, West Greenland in July 1998.

Plate 1: Photomicrograph (x200) of *Aulocomnium turgidum* (leaf)

Plate 2: Photomicrograph (x200) of unidentified Bryophyta species in faeces of a Greenland White-fronted Goose at the sympatric site

Plate 3: Photomicrograph (x200) of *Sphagnum squarrosum* (leaf)

Plate 4: Photomicrograph (x200) of unidentified Bryophyta species in faeces of a Greenland White-fronted Goose at the sympatric site

Plate 5: Photomicrograph (x200) of *Equisetum arvense* (leaf)

Plate 6: Photomicrograph (x200) of Equisetaceae species in faeces of a Canada Goose at the sympatric site

Plate 7: Photomicrograph (x200) of *Luzula confusa* (lower leaf)

Plate 8: Photomicrograph (x200) of Poaceae (*Luzula* sp.) in faeces of a Canada Goose at the sympatric site

Plate 9: Photomicrograph (x200) of *Carex rariflora* (lower leaf)

Plate 10: Photomicrograph (x200) of unidentified Cyperaceae species in faeces of a Greenland White-fronted Goose at the allopatric site

Plate 11: Photomicrograph (x200) of *Cerastium alpinum* (lower leaf)

Plate 12: Photomicrograph (x200) of unidentified Dicotyledones species in faeces of a Canada Goose at the allopatric site

Photomicrograph (x200) of *Aulacomnium turgidum* (leaf).

Photomicrograph (x200) of unidentified Bryophyta species in faeces of a Greenland White-fronted Goose at the sympatric site.

Photomicrograph (x200) of *Sphagnum squarrosum* (leaf).

Photomicrograph (x200) of unidentified Bryophyta species in faeces of a Greenland White-fronted Goose at the sympatric site.

Photomicrograph (x200) of *Equisetum arvense* (leaf).

Photomicrograph (x200) of Equisetaceae species in faeces of a Canada Goose at the sympatric site.

Photomicrograph (x200) of *Luzula confusa* (lower leaf).

Photomicrograph (x200) of Poaceae (*Luzula* sp.) in faeces of a Canada Goose at the sympatric site.

Photomicrograph (x200) of *Carex rariflora* (lower leaf).

Photomicrograph (x200) of unidentified Cyperaceae species in faeces of a Greenland White-fronted Goose at the allopatric site.

Photomicrograph (x200) of *Cerastium alpinum* (lower leaf).

Photomicrograph (x200) of unidentified Dicotyledones species in faeces of a Greenland Canada Goose at the allopatric site.