

AES 395: ENVIRONMENTAL BIOLOGY RESEARCH PROJECT

LITERATURE REVIEW & METHODOLOGY

Project Title: Inter-Specific Competition And Habitat Exploitation Of Moulting
Geese In West Greenland

Author Name: N. S. Jarrett

Degree: Environmental Biology

Project Supervisor: Dr A. J. Richards

Date: February 1999

Tutor: Dr Ollerenshaw

AES 395: ENVIRONMENTAL BIOLOGY RESEARCH PROJECT

LITERATURE REVIEW & METHODOLOGY

Project Title: Inter-Specific Competition And Habitat Exploitation Of Moulting
Geese In West Greenland

Project Supervisor: Dr A. J. Richards

Module Leader: Dr. A. J. Richards

Deadline Date: May 1999

Author Name: N. S. Jarrett

Degree: Environmental Biology

Tutor: Dr Ollerenshaw

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

Part One: A review of inter-specific competition in wildfowl species

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 individual organisms 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, larger herbivores are deprived use of winter productivity, but the effect on 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 being 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 and Macdonald, 1995). Evidence of competition (e.g. for food) between two species can be achieved by comparing 'actual' niche breadth (realised niche) (dietary variation in sympatric populations) (Clode & Macdonald, 1995). Therefore, 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 arrival of a new, closely related species will offer prime opportunity to study potential for competition and its effect on the inhabitant in a natural environment. However, this is rarely possible to study in nature, but has been done in some species (e.g. Fabricius *et al.*, 1974; Code and Macdonald 1995).

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.

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.

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, and 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.

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) by 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, but 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 is only weakly indicative of competition. Invariably Type I evidence provides an indication that competition is occurring or has occurred, but relies on observations which are difficult to test rigorously. 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).

Type II Evidence

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

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 - prey size decreasing as the water column was descended.

Comparable observations have been made by Siegfried (1976): diving ducks obtained very similar diets from different sites in the 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) Eadie *et al.* (1979) demonstrated that dabbling wildfowl species exhibit inverse relationships between similarities in body size and similarities in foraging behaviour, while 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.

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, abiotic 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).

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. For example, the range expansion of the mallard *Anas platyrhynchos* into the north-east USA has been presumed to be the cause and effect of a declining Black duck *Anas rubripes* population, but it is very probable that habitat change has played no small part in the recent fortunes of both species (Ankney *et al.*, 1986; Jarrett, *in press*).

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 feed 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 flocks 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.

PART TWO

GEESE IN WEST GREENLAND

INTRODUCTION

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. Frimer & Nielsen, 1990; Boertman, 1994; Bennike, 1990; 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.*, press). For example, it may be hypothesised that population regulation may 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. pre-breeding and during brood-rearing, and faecal analyses have shown that birds generally select for high quality vegetation, which is often in short supply in the arctic (e.g. Alisauskas & 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.

INTER-SPECIFIC COMPETITION BETWEEN GEESE

Schoener (1983) observed that generally, large species are more likely to out-compete smaller species. The Canada goose race which is colonising Greenland is larger than the White-fronted Goose (Palmer, 1976; Cramp & Simmons, 1986; Fox *et al.*, 1996; Jarrett & Warren, 1998) and there is evidence that both goose species exploit similar habitat in the tundra landscape of West Greenland (Wright & Mitchell, 1993; Fox *et al.*, 1996; Kristiansen, 1998). Since West Greenland has hitherto only been exploited by White-fronted geese, 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, and recently recorded inverse relationship of population size in Isunngua (i.e. Canada geese have

increased, while White-fronts have decreased in numbers) are observations that may be invoked as Type I and Type II evidence for competition, respectively. However, observations such as these 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. While competition can occur and may affect the species in many ways, perhaps the most obvious way concerns food selection, inviting the question do these geese have similar food preferences?

While a few studies on the diet of the Greenland White-fronted goose have been undertaken on the breeding grounds (Madsen & Fox, 1981), nothing is known about the feeding behaviour of Canada geese in West Greenland. If for example, food competition occurs between White-fronted geese 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.

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 - to be inserted*). 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 - to be inserted*):

- 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 there edges a carpet of moss and were surrounded by steep slopes with vegetation comprising grasses, sedges and hummocks of *B. nana* and *S. glauca*.

Habitat Use

Habitat utilisation was measured by assessing dropping (faeces) densities in different areas used by feeding geese. Counts of faeces were made along 100 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.

Food selection and vegetation analysis

In order to assess diet, fresh faecal pellets and 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 in paper bags for later laboratory analysis. Following the procedure of Owen (1975) diet composition was determined by sampling the relative frequency of plant fragments at 100 random points on 10 microscope slides viewed at 100-400x magnification. Diet was assessed in this way for each goose species in each situation (i.e. allopatric and sympatric situations).

To identify the plant fragments, reference specimens were collected from each site and dried in a press. In the laboratory, epidermal surfaces were photographed under the microscope at 100-400x magnification. Plant fragments were identified to generic level where possible, but subsequently pooled in to the following main taxonomic groups: grasses (Poaceae), sedges

(Cyperaceae), rushes (Juncaceae), mosses (Bryophyta), Equisetum (Equisetaceae) and Dicotyledones.

Vegetation analysis

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.

Based on the pin-point results, percentage occurrence of the main food plant groups was estimated. In order to investigate diet selectivity, I calculated Manly's alpha preference index (Krebs, 1989) 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:

$$\alpha_i = \text{Manly's alpha (preference index) for prey type } i$$

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.

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

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 of resource use).

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' peck rate and step rate were recorded; when birds were on the water, inter-bird distances were estimated (in goose-lengths); when on land, birds' distance from the water's edge was estimated (in goose lengths). All goose-geese/ goose-caribou, *Rangifer tarandus*, interactions were recorded. To reflect the physical condition of the geese abdominal profiles were scored regularly.

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.

REFERENCES

- ALTMAN, J.** 1974. *Observational study of behaviour: sampling methods*. Behaviour 49: 227-267.
- ABRAMS, P. A.** 1977. *Density-independent mortality and interspecific competition: a test of Pianka's niche overlap hypothesis*. American Naturalist 111:539-552.
- AFTON, A. D. & S. L. PAULUS.** 1992. *Incubation and brood care*. In: BATT, B. D. J., AFTON, A. D., ANDERSON, M.G., ANKNEY, C. D. JOHNSON, D. H., KADLEC, J. A. & G. L. KRAPU (Editors). *Ecology and management of breeding waterfowl*. University of Minnesota Press. Minneapolis, USA.
- ALISAUKAS, R.T. & C.D. ANKNEY.** 1992. *The cost of egg laying in relationship to nutrient reserves in waterfowl*. In: BATT, B. D. J., AFTON, A. D., ANDERSON, M.G., ANKNEY, C. D. JOHNSON, D. H., KADLEC, J. A. & G. L. KRAPU (Editors). *Ecology and management of breeding waterfowl*. University of Minnesota Press. Minneapolis, USA.
- ANKNEY, C. D., DENNIS, D. G. & R. C. BAILEY.** 1987. *Increasing mallards, decreasing American Black Ducks: coincidence or cause and effect?* Journal of Wildlife Management 51: 523-529.
- BARNES, G. G & V. G. THOMAS.** 1987. *Digestive organ morphology, diet and guild structure of North American Anatidae*. Canadian Journal of Zoology 65: 1812-1817.

- BEGON M., HARPER J. L. & C. R. TOWNSEND.** 1996. *Ecology: Individuals, populations and communities*, Blackwell Scientific Press, Oxford, UK.
- BENNIKE, O.**1990. *Observations of geese and other birds in West Greenland 1989 and 1990*. Dan. Ornthol. Foren. Tidsskr. 84:145-150.
- BOERTMANN, D.** 1994. *An annotated checklist of the birds of Greenland*. Meddelser om Grønland, Bioscience 38:1-63.
- BRANDL, R. & K. SCHMIDTKE.** 1983. *Invasion by tufted ducks Aythya fuligula into a pond area: implications of diffuse competition*. Oecologia 59: 397-401.
- CHARNOV, E. L. ORIAN, G. A. & K. HYATT.** 1976. Ecological implications of resource depression. American Naturalist 110: 247-259.
- CLODE, D. & D. W. MACDONALD.** 1995. *Evidence for food competition between mink (Mustela vison) and otter (Lutra lutra) on Scottish islands*. Journal of the Zoological Society of London 237: 435-444.
- COTTAM C.** 1939. *Food habits of North American diving ducks*. U.S. Department of Agriculture Technical Bulletin No. 643.
- CONNELL, J. H.** 1961. *The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus*. Ecology 42: 710-23.

- CONNELL, J.H.** 1983. *On the prevalence and relative importance of interspecific competition: evidence from field experiments*. *American Naturalist* 122:661-696.
- COULTER M. W.** 1955. *Spring food habits of surface-feeding ducks in Maine*. *Journal of Wildlife Management* 19:263-267.
- CRAMP, S. & K. E. L. SIMMONS.** (Editors). 1985. *Handbook of the Birds of Europe, the Middle East and North Africa. Volume I: Ostrich To Ducks*. Oxford University Press, Oxford.
- EADIE J., Mc A., NUDDS, T. D. & C. D. ANKNEY.** 1979. *Quantifying interspecific competition in foraging behaviour of syntopic Anas (Anatidae)*. *Canadian Journal of Zoology* 57: 412-415.
- EBBINGE, B.** 1985. *Factors determining the population size of arctic breeding geese, wintering in Western Europe*. *Ardea* 73:121-128.
- FABRICIUS, E., BYLIN, A., FERNO A, & A. RADESATER.** 1974. *Intra- and inter-specific territorialism in mixed colonies of the Canada goose Branta canadensis, and the Greylag goose Anser anser*. *Ornis Scandinavica*. 510:25-35.
- FOX, A. D. & D. A. STROUD.** 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., & H. J. WILSON.** 1994. *Greenland White-fronted geese in Ireland and Britain 1982/83-1993/94*. *Greenland White-fronted Goose Study*

Research Report No. 8. Greenland White-fronted Goose Study and National Parks and Wildlife Service of The Office of Public Works, Dublin.

FOX, A. D., GLAHDER, C., MITCHELL, C. R., STROUD, D. A., BOYD H. & J, FRIKKE. 1996. *North American Canada Geese (Branta canadensis) in West Greenland*. The Auk 113 (1):121-233.

FRIMER, O. & S. M. NIELSEN 1990. *Bird observations in Aqajarua-Sullorsuaq, Disko, West Greenland, 1989*. Dan. Ornthol. Foren. Tidsskr. 84:151-158.

GAUSE, G. F. 1934. *The struggle for existence*. Hafner, New York, USA.

HOHMAN, W. L., ANKNEY, C. D. & D. H. GORDON. 1992. *Ecology and management of postbreeding waterfowl*. In: BATT, B. D. J., AFTON, A. D., ANDERSON, M.G., ANKNEY, C. D. JOHNSON, D. H., KADLEC, J. A. & G. L. KRAPU (Editors). *Ecology and management of breeding waterfowl*. University of Minnesota Press. Minneapolis, USA.

HUEY, R. B. 1979. *Parapatry and niche complementarity of Peruvian desert geckos (Phyllodactylus): the ambiguous role of competition*. Oecologica 38: 249-259.

HUTCHINSON, G. E. 1959. *Homage to Santa Rosalia; or, Why are there so many kinds of animals?* American Naturalist 93: 145-159.

KRAPU G. L. & K. J. REINECKE 1992. *Foraging ecology and nutrition*. In: BATT, B. D. J., AFTON, A. D., ANDERSON, M.G., ANKNEY, C. D. JOHNSON, D. H., KADLEC, J. A.

& G. L. KRAPU (Editors). *Ecology and management of breeding waterfowl*. University of Minnesota Press. Minneapolis, USA.

KREBS, C. J. 1989. *Ecological methodology*. Harper Row. New York.

KRISTIANSEN, J. N. 1998. (Editor). *Report of the 1997 Ringing Expedition to Isunngua, West Greenland*. Report to the Greenland White-fronted Goose Study. Copenhagen.

JARRETT N. S. & S. M. WARREN. 1998. *Morphometrics*. In: KRISTIANSEN, J. N. 1998. (Editor). *Report of the 1997 Ringing Expedition to Isunngua, West Greenland*. Report to the Greenland White-fronted Goose Study. Copenhagen.

JARRETT N. S. (accepted) *The North American Black Duck. Anas rubripes*. In KEAR, J. (Editor) *Wildfowl - Bird Families of the World Series* (in preparation).

LACK, D. 1947. *Darwin's Finches*. Cambridge University Press, Cambridge, UK.

LACK, D. 1971. *Ecological isolation in Birds*. Blackwell Scientific Publications, Oxford, UK.

LACK, D. 1974. *Evolution illustrated by waterfowl*. Blackwell Scientific Publications, Oxford, UK.

LEHNER, P. N. 1979. *Handbook of ethological methods*. STPM Press, Garland, New York.

MACARTHUR, R. H. 1972. *Geographical Ecology: patterns in the distribution of species.*
Harper Row, New York, USA.

MADSEN J. 1987. *Status and management of goose populations in Europe, with special reference to populations resting and breeding in Denmark.* Dan. Rev. Game Biol. 12(4):76.

MADSEN J. 1991. *Status of goose populations in the Western Palearctic in the 1980's.*
Ardea 79 (2):113-122.

MADSEN, J. & A. D. FOX, 1981. *The summer diet of the Greenland White-fronted Goose.*
In: FOX, A.D. & D.A. STROUD. 1981. Report of the 1979 Greenland White-fronted Goose
Study Expedition to Eqaungmiut Nunat, West Greenland. 108-115.

MADSEN, J. & C. E. MORTENSEN. 1987. *Habitat exploitation and interspecific competition of moulting geese in East Greenland.* Ibis 129: 25-44.

MADSEN J., BREGNBALLE, T. & A. HASTRUP. 1992. *Impacts of the Arctic fox, Alopex lagopus on nesting success of geese in Southeast Svalbard, 1989.* Polar Research 11(2): 35-39.

MADSEN J., REED, A. & A. ANDREEV. 1996. *Status and trends of geese (Anser sp., Branta sp.) in the world: A review, updating and evaluation.* In: MIRKAN. M., (Editor) Proc. Anatidae 2000. Conference, Strasbourg 1994. Gibier Faune Sauvage, Game Wildl. Special Anatidae 2000.

MAYHEW, P. & D. HOUSTON. 1999. *Effects of winter and early spring grazing by Wigeon Anas penelope on their food supply.* Ibis 141(1): 80-84.

NEWTON, I. 1998. *Population Limitation in Birds.* Academic Press Limited, London, UK.

NUDDS, T.D. 1981. *Effects of coots on duck densities in Saskatchewan parkland.* Wildfowl 32. 64: 19-22.

NUDDS, T. D. 1983. *Niche dynamics and organisation of waterfowl guilds in variable environments.* Ecology. 64: 19-330.

NUDDS, T. D. 1992. *Patterns in breeding duck communities.* I In: BATT, B. D. J., AFTON, A. D., ANDERSON, M.G., ANKNEY, C. D. JOHNSON, D. H., KADLEC, J. A. & G. L. KRAPU (Editors). *Ecology and management of breeding waterfowl.* University of Minnesota Press. Minneapolis, USA.

NUDDS, T. D., ABRAHAM, K. F., ANKNEY, C. D. & P. D. TEBBEL. 1981. *Are size gaps in dabbling- and wading bird arrays real.* American Naturalist 118: 549-552.

NUDDS, T. D. & J. N. BOWLBY. 1984. *Predator-prey size relationships in North American dabbling ducks.* Canadian Journal of Zoology 62: 2002-2012.

OWEN, M. 1975. *An assessment of faecal analysis technique in waterfowl feeding studies.* Journal of Wildlife Management 39 (2):271-279.

PALMER, R. S. 1976. (Editor). *Handbook of the North American birds. Volume 2.* Yale Univ. Press. New Haven, Connecticut, USA.

PARK, T. 1954. *Experimental studies of interspecific competition. II Temperature, humidity and competition in two species of Tribolium.* Physiological Zoology 27: 177-238.

PIANKA, P. 1976. *Competition and niche theory.* In: MAY, R.M. (Editor) *Theoretical ecology. Principles and applications:*114-141. Blackwell Scientific Press, Oxford, UK.

PÖYSA, H. 1983a. *Resource utilisation pattern and guild structure in a waterfowl community.* Oikos 40: 295-307.

PÖYSA, H. 1983b. *Morphology-mediated niche organisation in a guild of dabbling ducks.* Ornis Scandinavia 14:317-326.

PÖYSA, H. 1985. *Circumstantial evidence of foraging interference between two species of dabbling ducks.* Wilson Bulletin 97: 541-543.

PÖYSA, H. 1986. *Foraging niche shifts in multispecies dabbling duck (Anas spp.) feeding groups: harmful and beneficial interactions between species.* Ornis Scandinavia 17: 333-346.

SALMONSEN, F. 1950. *Gronlands Fugle. The birds of Greenland.* Munksgaard, Kobenhavn.

SALMONSEN, F. 1967. *Fuglene pa Gronland.* Rhodos, Kobenhavn.

SALMONSEN, F. 1990. *Gronlands fauna*. Gyldendal, Kobenhavn.

SAVARD, J.-P. L. 1984. Territorial behaviour of Common Goldeneye, Barrow's Goldeneye and Bufflehead in areas of sympatry. *Ornis Scandinavia* 15: 211-216.

SAVARD, J.-P. L. & J. M. N. SMITH. 1987. *Interspecific aggression by Barrow's Goldeneye: a descriptive and functional analysis*. *Behaviour* 102: 168-184.

SAVARD, J.-P. L. 1988. *Winter, spring and summer territoriality in Barrow's Goldeneye: characteristics and benefits*. *Ornis Scandinavia* 19: 119-128.

SCHOENER, T. W. 1974. *Resource partitioning in ecological communities*. *Science* 185: 27-39.

SCHOENER, T. W. 1983. *Field experiments on interspecific competition*. *American Naturalist* 122:240-285.

SIEGFRIED, W. R. 1976. *Segregation of feeding behaviour of four diving ducks in southern Manitoba*. *Canadian Journal of Zoology* 54: 730-736.

SUTHERLAND, W. J. & G. A. ALLPORT. 1994. *Spatial depletion model of the interaction between Bean Geese and Wigeon with the consequences for habitat management*. *Journal of Animal Ecology* 63: 51-59.

SWANSON G. A., KRAPU, G. L & J. R. SERIE. 1979. *Foods of laying female dabbling ducks on the breeding grounds*. In BOOKHOUT, T. A. (Editor). *Waterfowl and wetlands - an*

integrated review. Pp 47-85. The Wildlife Society, Proceedings 1977 Symposium, Madison, Wisconsin N.C. Section.

TOFT, C. A., TRAUGER, D. L. & H. W. MURDY. 1982. *Tests for species interactions: breeding phenology and habitat use in subarctic ducks*. *American Naturalist* 120: 586-614.

WIENS, J. A. 1989. *The Ecology of Bird Communities. Volume 2: Processes and Variations*. Cambridge University Press, Cambridge, UK.

WIENS J. A. & J. T. ROTENBERRY. 1981. *Morphological size ratios and competition in ecological communities*. *American Naturalist* 117: 592-599.

WRIGHT, G. & C. MITCHELL. 1993. *Report of the 1992 expedition to Isungua, West Greenland*. Greenland White-fronted Goose Study, Aberystwyth, UK.

Activity budget studies have also revealed that different duck species feed in distinct and different ways. Smaller species such as Teal *Anas crecca* spent a lot of time dabbling at the surface, whereas larger species, such as mallards, *Anas platyrhynchos* spend more time upending. This suggests that the resources used by ducks are partitioned spatially and access is facilitated by different neck lengths (Sjöberg & Danell, 1981), a simple observation which may indicate competition.

In Western Greenland only the Greenland White-fronted Goose *Anser albifrons flavirostris*, historically bred in the low arctic region (Salmonsén, 1950, 1967, 1990). However, records of Canada Goose, in this part of the country are known since last century (Salmonsén, 1950). Until recently, these observations were mainly from the Disko Bay area (e.g. Salmonsén 1950, 1967, 1990; Frimer & Nielsen 1990; Boertman 1994; Boertmann, 1994; Bennike 1990; Fox *et al.*, 1996). The Canada goose has now colonised several areas in the Disko Bay area and is now more common than the White-fronted geese (Bennike, 1990). The expansion continues further south (Boertmann, 1994; Fox *et al.*, 1996) and in 1988 a survey of White-fronted geese in the Isunngua area (67°05'N, 50°30'W) north of Kangerlussuaq (Søndre Strømfjord), West Greenland, found 12 Canada geese including two fledged goslings. Relatively little increase occurred in that area in the following six years (Wright & Mitchell 1993; Fox *et al.*, 1996) until in 1995 more than 100 Canada geese were found including several families (A.D. Fox *personal communication*). Similar numbers were observed in 1996 when the proportion of breeding pairs and goslings was even higher than previously (J. Kristiansen *personal communication*), and in 1997 c 200 Canada geese were recorded in the area: the highest number hitherto (Kristiansen 1998). This is striking since numbers of Canada geese now exceed the number of White-fronted geese in the same area. In addition, at some traditional White-fronted goose breeding sites only Canada goose families were observed during the 1997 survey and ringing expedition (D. Stroud *personal communication*). Detailed behavioural observations of moulting (i.e. flightless) birds feeding in sympatric flocks in Isunngua, have shown that Canadas are superior to White-fronts (personal observation).

The presence of both species in the Isunngua area offers a unique opportunity to study the phenomenon of inter-specific competition between closely related species from the very beginning of immigration and expansion of the new arrival. It is interesting to speculate whether the sudden arrival and expansion of the Canada goose will affect the White-fronted goose in West Greenland. Large herbivores such as geese spend much time feeding, especially during crucial periods, e.g. pre-breeding and during brood-rearing. During these periods birds select for high quality vegetation which often is in short supply in the arctic (e.g. Alisauskas & Ankney, 1992; Afton & Paulus, 1992; Hohman *et al.*, 1992). For that reason it might be expected that some inter-specific interaction may occur. Since this part of Greenland has hitherto only been exploited by White-fronted geese, we must assume that this species utilises its fundamental niche. Fortunately a few reference studies describing the habitat use are available (Madsen & Fox, 1981; Fox & Stroud, 1988). According to Schoener (1983) large species are more likely to out-compete smaller species and the Canada goose race present in the area is larger than the Greenland White-fronted Goose (Palmer, 1976; Cramp & Simmons, 1986; Fox *et al.*, 1996, Jarrett & Warren 1998). Hence, for this reason the Canada geese might be superior to the White-fronted goose.

METHODS

an be measured is represents a Diamond studied species living on islands

It is a general ecological principle that whenever resources are in limited supply, species with identical needs cannot persist together indefinitely (Gause 1934; Begon *et al.*, 1996). Where resources are finite, competition between two or more species may act to control their distribution and abundance. Invariably those species which are either best adapted, or most efficient at exploiting the limiting resource will out-compete the other leading to differences in distribution, habitat-utilisation or feeding ecology (Lack 1947, 1971). Therefore, inter-specific competition arising from the joint use of a limited resource by two or more species (Pianka, 1976) is often portrayed as an evolutionary force, driving species divergence and influencing the composition and structure of communities (MacArthur 1972; Wiens 1989; Nudds, 1992; Begon *et al.*, 1996).

The essence of inter-specific competition is that individuals of one or both species, suffer reduced fecundity, survivorship or growth as a result of resource exploitation or interference by individuals of other species (Begon *et al.*, 1996). In any pair of competing species, it is rare for both to suffer equally, and the effects of competition are usually asymmetric, affecting one species more heavily than the other (Charnov *et al.* 1976; Newton 1998). However, competing species do not always affect each other negatively: vulture species which find their food by watching the behaviour and movement of other foraging species serve as an example where species may interact without suffering adversely from a shared resource (Houston 1988). In exploitation competition, individual organisms indirectly deprive others of resources by using and therefore reducing, the amount of resources available to their competitors. Sutherland & Allport (1994) showed that an increasing wintering population of herbivorous Wigeon *Anas penelope* grazed swards on a reserve in south-east England to such low levels that Bean geese *Anser fabalis*, the species for which the reserve was established

and managed, were forced to exploit alternative feeding opportunities in pastures away from the reserve. While the Wigeon did not cause the goose population size to decline, exploitation competition was the mechanism which caused geese to shift their habitat use.

Interference competition occurs when one species physically excludes the other from access to one or more resources. Both territoriality and kleptoparasitism (piracy) are forms of interference competition. Although inter-specific territoriality is rare in birds (Krapu & Reinecke 1992) this form of interference has been identified as the cause for observed allopatry in species of the duck genus *Bucephala* (Savard 1984). Studies of the Barrow's goldeneye *Bucephala islandica* suggest that interference behaviour functions specifically to reduce competition for food such that the degree of aggression shown by male goldeneye correlated strongly to the degree of potential dietary overlap with the intruding species (Savard & Smith 1987; Savard 1988). Kleptoparasitism has been studied in American wigeon *Anas americana* and Gadwall *Anas strepera* two dabbling duck species which regularly steal aquatic vegetation from American Coot *Fulica americana*. The latter can dive to depths of 3 m in order to collect submerged vegetation which is then ingested at the surface. When approached by potential pirate species, coots readily drop their spoils, and so kleptoparasitic ducks are able to obtain food plants which ordinarily they could not obtain themselves. Although coots are capable of being very aggressive, they seldom attack the ducks and this may be because aggressive interactions are expensive in terms of post-aggression movements (i.e. extensive bouts of preening) (Amat & Soriguer 1984). Nudds (1981) could not find an inverse correlation between population sizes of coots and any of 10 species of dabbling ducks, which could indicate the effects of competition.

The outcome of competitive interactions may manifest in terms of niche shift along one of the dimensions defining the species' niche, although a 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 achieved by comparing realised niche breadth in sympatric and allopatric populations. Therefore, 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; Connell 1983; Schoener 1983).

Evidence of niche shifts have been observed experimentally in mixed flocks of titmice (Paridae) and Goldcrests *Regulus regulus*. Suhonen *et al.*, (1992) observed that in the coniferous forests of northern Europe, dominant Willow tits *Parus montanus* and Crested tits *P. cristatus* forage at sites within trees, while the smaller Coal tits *P. ater* and Goldcrest appear to be confined mainly to the outer twigs where there is greater risk of predation. Reduction in numbers of the dominant species in three experimental plots, resulted in individuals of the subordinate species shifting their foraging activity to the inner canopy, (Alatalo *et al.* 1985). The spatial separation of species was presumed to be due to interference competition because the larger congeners were often observed chasing the smaller species. However, when the two subordinate species were experimentally removed with the result that food supplies in the peripheral parts of trees were less depleted, the dominant species altered their foraging behaviour and began to spent significantly more time feeding on outer twigs (Alatalo *et al.* 1987). Thus the feeding sites used by each species appeared to be reduced in sympatry as a consequence of combined interference and exploitation inter-specific competition.

Competition may also occur across orders of taxa. After the removal of fish from a 17 hectare lake in southern England, submerged plant cover increased from less than 1% to 95% of the lake surface, while population sizes of benthic invertebrates doubled (Phillips 1992).

Wildfowl herbivores including Mute swan *Olor olor*, Coot *Fulica atra* and Gadwall *Anas strepera* increased in association with greater weed growth, and use by Shoveler *Anas spatula* and Pochard *Aythya ferina* in association with greater invertebrate numbers. Mallard *Anas platyrhynchos* duckling survival also improved (Wright & Phillips 1990). Such changes were not seen in other lakes nearby whose fish populations were left intact. Similarly in Sweden it has been observed that Goldeneye *Bucephala clangula* preferred lakes without fish to those with fish, and the diets of birds and fish overlapped. After fish were removed from one lake and prey species increased, more Goldeneye were seen feeding there than formerly, and more than on an adjacent control lake (Eriksson 1979).

Other experiments on birds have investigated the effects of inter-specific competition on fecundity and survival of individuals. Hogstedt (1980) observed that Magpies *Pica pica* and Jackdaws *Corvus monedula* breeding in Southern Sweden used the same food resource. Since chicks often starved in the nest, he hypothesised that food was limiting species' reproductive success. In order to elucidate the mechanism of competition, Hogstedt enticed hole-nesting Jackdaws to breed within Magpie territories by providing nest boxes. As a control, Jackdaws were discouraged from breeding in some Magpie territories, and to remove the effects of differences in Magpie pair- or territory-quality, nest boxes were re-located from experimental to control sites between years. The results demonstrated that Magpies breeding in sympatry with Jackdaws suffered significantly reduced breeding success in terms of the number and the quality (assessed by weight) of young produced, when compared to those pairs breeding in allopatry. This difference in realised fitness was attributed to increased starvation of chicks

due to food depletion in Magpie territories by Jackdaws, and to increased predation of nest contents by Hooded Crows *C. corone*. Sympatric Magpies were forced to spend less time at the nest and more time searching for food and this enabled predatory Carrion crows to locate nestlings producing hunger induced calls.

Competition is manifested in terms of niche shifts along one of the dimensions defining the species' niche. Although a 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 achieved by comparing the realised ('actual') niche breadth of species such as dietary variation in sympatric populations (Clode & Macdonald, 1995). Therefore, 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). Hence the arrival of a new, closely related species offers an prime opportunity to study the potential for competition and its effect on the inhabitant in a natural environment. However, opportunities for study have been few: Fabricius *et al.*, (1974) studied intra- and inter-specific territorialism in mixed colonies of the Canada goose *Branta canadensis*, and the Greylag goose *Anser anser*, and Clode & Macdonald (1995) observed the effects of invading mink, *Mustela vison*, on native otter *Lutra lutra*, populations living on the Western Isles of Scotland.

The consequences of competition are best shown by experiments in which the population size of species are artificially altered. The response to changes in numbers can be measured as changes in feeding efficiency and habitat utilisation or as changes in fecundity or survival rate in the inferior species. Whereas the first response is typical where one species is constrained by another

The phenomenon of inter-specific competition has long been recognised, especially in the context of its importance in the shaping of communities and species. This has been discussed by various authors (e.g. Begon *et al.*, 1996; Nudds, 1992). The term inter-specific competition refers to the joint use of a limited resource by two or more species (Pianka, 1976), and therefore competition can only occur if a resource is in limited supply, (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. The essence of inter-specific competition is that individuals of one species (or both) suffer reduction in fecundity, survivorship or growth as a result of resource exploitation or interference by individuals of another species (Begon *et al.*, 1996). Consequently, 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 and Macdonald, 1995). Evidence of competition (e.g. for food) between two species can be achieved by comparing 'actual' niche breadth (realised niche) (dietary variation in sympatric populations) (Clode & Macdonald, 1995). Therefore, 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). Hence the arrival of a new, closely related species will offer prime opportunity to study potential for competition and its effect on the inhabitant in a natural environment. However, this is rarely possible to study in nature, but has been done in some species (e.g. Fabricius *et al.*, 1974; Clode and Macdonald 1995).

By adopting an experimental approach in which the population numbers of one species are changed it has been possible to conduct field studies demonstrating inter-specific competition and its effects in a range of organisms (). Measurable responses to altered numbers include changes in feeding rate or niche shifts, particularly in situations where a dominant species is greatly reducing the feeding rates of a subordinate species.

Feeding

Dominant species can

which combine to alter the population

Huey 1979 Type 1

Experimental approaches have n

OBJECTIVES

The primary objectives are:

1. To assess habitat use by breeding and non-breeding White-fronted geese and Canada geese in the Isunngua area of West Greenland in the period May to August 1998.
2. To monitor all interactions between the two species during this period.
3. To survey the Isunngua region in order to obtain data on population sizes of all breeding and non-breeding wildfowl species, in late July/early August 1998.

Figure 1 shows the proposed location of the study area in West Greenland. Figure 2 shows the location, within the study area, where the two species of geese were caught and marked with neck collars and leg bands in 1992 and 1997.

METHODS

The fieldwork will take place in the Isunngua area, Kangerlussuaq. Due to previous visits we know of the occurrence of both allopatric and sympatric goose sites. Study areas will thus comprise:

1. Only White-fronted geese (allopatric)
2. Only Canada geese (allopatric)
3. Co-existing White-fronted and Canada Geese (sympatric)

In 1997, 125 Canada geese and 40 White-fronted Geese were individually marked. Thus, it should be possible to follow individual birds during the 1998 rearing period. At each site the following methodology will be applied:

- Visual observations of feeding strategy (pecking or grubbing) will be performed to assess whether above-ground or below-ground organs of plants are preferred.
- Time budgets will be carried out to analyses for differences in activities between sites.
- To assess differences in habitat (including nest sites) all possible variables will be measured in the field; altitude, distance to water (lakes or streams), distance to feeding sites, plant community category. In addition, a relative estimate of predator presence will be measured (Madsen *et al.*, 1992).
- The variables will subsequently be analysed by means of a multivariate model.
- Goose droppings from adults and goslings each species, will be collected for later analysis at each feeding site.

- Plant reference material will be collected to aid identification of plant fragments in the droppings. Diet content will be determined following the microscopic quadrat sampling technique procedure (Owen, 1975).
- To assess niche breadth in the diet of the two species 'standard niche breadth' will be calculated using Levin's formula (Krebs 1989) for both allopatric and sympatric individuals.
- Niche overlap will then be calculated using Pianka's adaptation of MacArthur and Levins' formula (Krebs, 1989).

TIMETABLE

Table 1 shows the timetable of The Greenland Goose Project 1998. JK will arrive prior/simultaneously with the geese at the beginning of May. He will stay in Greenland for 16-17 weeks, and will monitor geese throughout their breeding cycle. By mid-August most geese will have departed the Isungua study area. NSJ will arrive prior to hatching of goslings and will remain until the beginning of August, by which time goslings will have fledged and all adults regained flight. Once families are 'on the wing' geese disperse from nest-site and initial rearing areas.

The interim report will be prepared by 31 December 1998. The final report will be completed by 31 May 1999. Various scientific papers will be prepared and submitted to relevant journals in due course.

REFERENCES

(Lack 1947, 1971). Therefore, 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 the divergence of species and influencing the composition and structure of communities (MacArthur 1972; Wiens 1989; Nudds, 1992; Begon *et al.*, 1996).

The limiting resource for which species may be in competition includes food, breeding sites, predator free-space, indeed any one of the dimensions defining the niche of a species (ref.).

Two types of inter-specific competition are recognised: interference and exploitation. In exploitation competition, individual organisms deprive others of resources indirectly by using and therefore reducing, the amount of resources available to the competitor. Interference competition occurs when one of two organisms physically excludes the other from access to resources. The essence of inter-specific competition is that individuals of one species, or both, suffer reduced fecundity, survivorship or growth as a result of resource exploitation or interference by individuals of other species (Begon *et al.*, 1996). However, in any pair of competing species, it is rare for both to suffer equally and so the effects of competition are usually asymmetric and affect one species more heavily than the other (Newton 1998). and kleptoparasitism are examples of interference competition

In field studies of inter-specific competition, the effects of competition can be shown by experimentally changing the numbers of one species (Connell 1983). Measurable responses to altered population sizes include changes in feeding rate or niche shifts, particularly in situations where a dominant species is greatly reducing the feeding rates of a subordinate species. Evidence of niche shifts have been observed experimentally in mixed flocks of

titmice and Goldcrests *Regulus regulus*. Suhonen *et al.*, (1992) observed that in the coniferous forests of northern Europe, dominant Willow tits *Parus montanus* and Crested tits *P. cristatus* forage at sites within trees, while the smaller Coal tits *P. ater* and Goldcrest appear to be confined mainly to the outer twigs where there is greater risk of predation. Reduction in numbers of the dominant species in three experimental plots, resulted in individuals of the subordinate species shifting their foraging activity to the inner canopy, (Alatalo *et al.* 1985). The spatial separation of species was presumed to be due to interference competition because the larger congeners were often observed chasing the smaller species. However, when the two subordinate species were experimentally removed with the result that food supplies in the peripheral parts of trees were less depleted, the dominant species altered their foraging behaviour and began to spend significantly more time feeding on outer twigs (Alatalo *et al.* 1987). Thus the feeding sites used by each species appeared to be reduced in sympatry as a consequence of combined interference and exploitation inter-specific competition.

or in survival or reproduction of the constrained species. experimental removal or addition of responses of species to The effects of competition have been shown experimentally

Consequently, 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 achieved by comparing the realised ('actual') niche breadth of species such as dietary variation in sympatric populations (Clode & Macdonald, 1995). Therefore, evidence for competition often comes from the contraction of a fundamental niche in the presence

However, competing species do not always affect each other negatively: vulture species which find their food by watching the behaviour and movement of other foraging species serve as an example where species may interact without suffering adversely from a shared resource (Houston 1988).

Kleptoparasitism has been studied in American wigeon *Anas americana* and Gadwall *Anas strepera* two dabbling duck species which regularly steal aquatic vegetation from American Coot *Fulica americana*. The latter can dive to depths of 3 m in order to collect submerged vegetation which is then ingested at the surface. When approached by potential pirate species, coots readily drop their spoils, and so kleptoparasitic ducks are able to obtain food plants which ordinarily they could not obtain themselves. Although coots are capable of being very aggressive, they seldom attack the ducks and this may be because aggressive interactions are expensive in terms of post-aggression comfort movements (i.e. extensive bouts of preening) (Amat & Soriguer 1984). Nudds (1981) could not find an inverse correlation between population sizes of coots and any of 10 species of dabbling ducks, which could indicate the effects of competition.

In

may be inferred from other types of Huey (1979) described

in experiments can be While controlled experimental approaches are able to demonstrate the effects of competition as quantifiable responses responses such as to Nevertheless, competition is particularly difficult to demonstrate under field conditions and evidence for its existence has been (Huey 1979).

represented in three scenarios hypotheses may be presented as:

1. Inverse relationships between similarity in diet and similarity in habitat use Niche complementarity
2. inverse relationships between relationships between diversity and ecological similarity (Niche overlap hypothesis)
3. inverse relationships between species' population sizes or inverse relationships between the abundance of species and their ecological uniqueness, since species that are distinct from others should compete least and hence be more abundant.

However, the lack of information about how the two species interact means that predicting the ultimate distribution of both species is difficult.

The Greenland White-fronted Goose was considered threatened in the late seventies but has since increased and recovered (Fox *et al.*, 1994). However, attention to this population is still needed. Furthermore, since most goose populations in both Nearctic and Palearctic regions have increased enormously, mainly because of restricted hunting and expanding feeding sites on the winter grounds, population regulating mechanisms are expected to occur in summer (breeding) grounds and information on this area of goose biology is almost completely lacking (Ebbinge, 1985; Madsen 1987, 1991; Madsen *et al.*, press). An important factor in this respect, therefore could be inter-specific competition. Apart from forming the basis of a comparative study between two species, it is likely that the field work will also provide new basic ecological information.