

Lack of competition between barnacle geese *Branta leucopsis* and pink-footed geese *Anser brachyrhynchus* during the pre-breeding period in Svalbard

Anthony D. Fox and Espen Bergersen

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The feeding ecology of barnacle geese and pink-footed geese was studied in Sassendalen, Svalbard during the pre-nesting period (late May) to assess the potential for inter-specific competition. Barnacle geese fed almost exclusively (97%) by grazing above-ground plant material, mostly (79%) along snow edges in moss-mat habitats. Pink-footed geese fed mostly (93%) by excavating below-ground parts of plants, mostly (56%) away from snow and were more evenly distributed between habitat types. Barnacle goose faeces contained mostly (62%) moss, that of pink-footed geese mostly (48%) below-ground plant storage organs (especially *Bistorta viviparum* L.). Principal components analysis of dropping contents showed no overlap in species diet in allopatry or sympatry. There was little overlap in diet and feeding ecology of the two species at this pre-nesting feeding site. Hence, unless increased goose feeding densities affect future vegetation density and composition, under present circumstances, increasing numbers of either species is unlikely to affect foraging conditions for the other at this important stage in the annual cycle. However, such changes could have local density-dependent intra-specific effects.

A. D. Fox (correspondence), Department of Wildlife Ecology and Biodiversity, National Environmental Research Institute, Kalø, Grenåvej 12, DK-8410 Ronde, Denmark. E-mail: tfo@dmu.dk. E. Bergersen, NINA, Polarmiljøseenteret, N-9296 Tromsø, and Institute of Biology, University of Tromsø, N-9037 Tromsø, Norway.

Most Western Palearctic arctic breeding goose populations have increased in the last 30 years (Madsen et al. 1999), elevating tundra grazing pressures which, combined with the effects of climate change, have the potential to modify tundra ecosystems (Jefferies and Rockwell 2002). A research initiative (Project FRA-GILE: Fragility of arctic goose habitat: impacts of land-use, conservation and elevated temperatures, <http://www.fragile-eu.net/>) was launched to investigate such processes following increases in numbers of Svalbard-

nesting geese. Increasing inter-specific interactions associated with changes in goose abundance and their effects at the population level have hitherto been rarely studied, despite the fact that inter-specific competition (resulting from direct interference or resource depletion, Goss-Custard 1980) is considered a major factor shaping distribution and abundance in avian communities (Newton 1998). However, direct asymmetry in exploitation of a resource limited in time and space can potentially dramatically affect the distribution and abundance of

co-occurring similar species (Keddy 2001). Increases in local goose densities may profoundly affect sympatric feeding behaviour, feeding distribution and access to favoured food items of a less aggressive species compared to allopatric situations (Kristiansen and Jarrett 2002). In that study, the more aggressive, invasive Canada goose *Branta canadensis* was behaviourally dominant over the endemic Greenland white-fronted goose *Anser albifrons flavirostris* at least during wing moult, ultimately resulting in local reductions and extinction of the white-fronted goose.

Hence, at critical times (when food resources are limited but crucial to meet specific needs during the annual cycle), competition for resources may have consequences for the carrying capacity of tundra vegetation for geese where more than one species is present. One such period is the prelude to nesting amongst barnacle *Branta leucopsis* and pink-footed *Anser brachyrhynchus* geese breeding in Svalbard. *En route* from wintering areas in Belgium, the Netherlands and Denmark, pink-footed geese stage in the Trøndelag area and Vesterålen, Norway in spring before flying direct to Svalbard (a final migration distance of c. 1100 km, Madsen et al. 1999). Svalbard-breeding barnacle geese winter in Scotland, and migrate via Helgeland and Vesterålen, mid-Norway c. 1400 km to the breeding areas (Madsen et al. 1999). Both species arrive in Svalbard after a prolonged, energetically expensive sea crossing (Butler and Woakes 1998). Shortly after arrival, females lay a full clutch of 4–5 eggs and incubate for 24–26 days (Owen 1980), both of which require considerable protein and energy resources. Goose species show a mixed capital/income breeding strategy, using both endogenous stores and exogenously derived nutrients in egg production (Gauthier et al. 2003). However, any pre-nesting nutrient supplement to female stores (depleted during spring migration to breeding grounds) is likely enhance the ability of an individual to invest in egg production and maintenance during incubation, and hence potentially affect her reproductive output. For this reason, access to good feeding opportunities during the period of rapid follicle development pre-nesting may benefit the reproductive outcome of individual geese. Furthermore, inter-specific interference at this time (when snow cover and frozen substrates limit availability and quality of plant material) may be expected to be more important at this stage of the annual cycle than at other times.

In this study, we describe the diet and behaviour of barnacle and pink-footed geese at a common feeding area during the immediate pre-nesting period (late May 2003) in Sassendalen, Svalbard to assess the degree of overlap in feeding distribution, feeding behaviour and diet. We also assess to what degree further increases in their numbers may affect the potential trajectories of both populations, based on these observations.

Methods

Study area and habitat types

The study area lay close to the northern gravel out-wash plain from the outflow of Brattlidalen on the northern side of Sassendalen (78°17'N, 17°07'E), a classic U-shaped glacial valley c. 4 km wide bisected by the braided fluvial channels of Sassenelva. The study area lay at the break of slope of the valley sides (400–500 m high) and comprised typical peri-glacial landscapes of largely alkaline Quaternary deposits (unconsolidated and sorted material, moraine deposits, gravel out-wash, fluvial and marine deposits). The vegetation was variable, but difficult to classify into communities at the beginning of the season when the study was undertaken. Habitats were assigned to four definable types based on evidence of above-ground litter from previous years, namely: (i) Grass-moss-drier moss mat, with abundant graminoids, (ii) Sedge and bare soil – dry ridge with *Carex rupestris* All., lichen, frequent *Bistorta viviparum*, often a mosaic mixed with heath or moss-dominated vegetation, and (iii) Moss mat – 100% moss, wet and soft at the time of the study with locally abundant *Dupontia* spp. and *Eriophorum scheuchzeri* Hoppe, and (iv) Dry heath slope – also with much moss, characterised by *Dryas octopetala* L., *Salix polaris* Wahlenb. and *Bistorta viviparum*.

Ambient temperature and conditions

Daily temperatures at Longyearbyen (c. 37 km west of the study site at the same altitude) ranged from -0.6°C to -1.7°C (minimum) and 0.0°C to 1.8°C (maximum), during the period 24–29 May 2003 when most of the observations were made. Snowmelt was well advanced, and under generally overcast conditions, with winds from $0-9\text{ m s}^{-1}$ (exceptionally up to 15 m s^{-1}), ablation was common, although surface running water was scant so early in the thaw.

Compilation of activity budgets

Birds were observed from a tent on a gravel ridge overlooking an area of some c. 1.8 km^2 of which initially c. 45% consisted of snow-free vegetation. From 22:00 h local time on 24 May 2003 for 24 hours, every half-hour, birds within this visually defined area were counted, assigned to habitat type (see above) and status (individual, paired or in groups), each individual assigned to an activity. We differentiated geese “grazing” (removing above-ground plant parts at or above the soil surface) from those “grubbing” (conspicuous probing below the soil surface to excavate and extract below-ground plant storage organs). Because continuous observations of the

same pair did not represent independent samples, mean feeding type for each focal pair was used as one sample to generate overall means and standard errors. Furthermore, additional opportunistic scan samples of foraging birds were made during 26–30 May to collect data on proportions grazing *vs* grubbing to validate the pair scan data. Males and females of both species were distinguished on the basis of relative size, behaviour and abdominal profile score (Owen 1981, Boyd and Fox 2003).

Faecal analysis

Plant epidermal fragments remain intact during passage through the alimentary canal of geese, enabling dietary analysis based on dropping contents (Owen 1975). Only very fresh droppings were collected in the field from the exact positions where geese had been observed feeding for at least one hour between 24 May and 2 June 2003. Flushed birds at the point of collection confirmed species responsible. At least ten individual droppings were gathered per sample, separated into sympatric areas (where both species had been feeding in the previous four hours) and allopatric areas where only one focal species had been present. Samples were dried in the field, returned to the lab, ground to powder, filtered (2 mm mesh) and analysed during December 2003–January 2004. Powder samples were eluted with water and mixed thoroughly, before subsamples were mounted on slides and examined microscopically. Food composition was quantified by determination of fragments following Owen (1975), sampling the first 100 fragments in 1 mm steps that fell within a 4 mm diameter circle inscribed on a graticule in the ocular. Attempts were made to identify each fragment by comparison with reference material (including above and below-ground parts) of all common plant species gathered from Sassendalen. Here, we amalgamated the observed fragments into eight broad categories, “moss”, *Equisetum*, “Dicotyledonous species”, “unidentified epidermis”, “graminoids”, *Salix* buds, *Bistorta/Oxyria* roots and “unidentified below-ground tissue” for analysis. Using Principal Components Analysis (PCA), each dropping collection was plotted according to their loadings on the first two axes.

Results

Feeding methods and distribution between species

Virtually all barnacle geese foraged by grazing (males $96.1\% \pm 1.35$ SE, $n=558$ observations of 30 different individuals, females $97.1\% \pm 0.91$, $n=823$ of 30 individuals). Most pink-footed geese foraged by grubbing (males $93.6\% \pm 1.97$, $n=442$ of 24 individuals, females

$93.0\% \pm 1.85$, $n=737$ of 27 individuals). Opportunistic scan samples of unsexed birds gathered daily from 26–30 May 2003 inclusive showed similar patterns (barnacle goose $98.4\% \pm 1.15$ SE grazing, $n=169$ observations, pink-footed goose $91.6\% \pm 2.58$ SE grubbing, $n=135$). Overall, $14.1\% (\pm 4.00$ SE, $n=766$ from 5 dropping collections) of pink-footed goose samples were large fragments of substrate, confirming the large amount of ingested soil material present. None was present in barnacle goose droppings, confirming the differences in the amount of above- and below-ground plant parts the two species were taking.

Although both species fed in the vicinity of melting snow, 78% of barnacle geese observations were within 0.5 m of the snow edge compared to 56% of pink-footed geese at distances greater than 0.5 m from snow. Both species foraged in all four habitat-types, although the majority of individuals exploited moss-mat vegetation. There was a significant difference in the distribution of the two species between the different habitat types ($\chi^2=285.8$, $df=3$, $P<0.001$). More than 60% of observations of barnacle geese were from moss-mat, while pink-footed geese were more evenly spread between the four different vegetation types.

Differences in diet between the two species

Both goose species foraged upon a range of plants, including *Equisetum* spp., dicotyledonous species and graminoids (Fig. 1). Moss predominated ($>60\%$) in barnacle goose faeces, whereas the below-ground storage organs of *Bistorta*, *Oxyria* and other (unidentified) species made up more than 50% of recorded species in pink-footed goose droppings (Fig. 1). *Equisetum* fragments in pink-footed goose faeces were predominantly brown (24 dark brown out of 34 identified fragments in four samples), but were exclusively green in barnacle goose faeces (no dark brown fragments out of 44 from

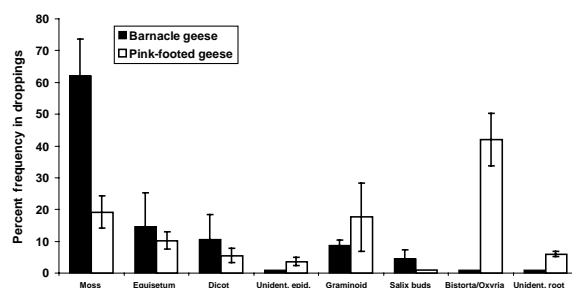


Fig. 1. Percentage frequency of different food items in the faecal material collected from barnacle (black histogram columns) and pink-footed geese (white histogram columns) using the pre-nesting feeding area at the mouth of Brattliddalen, Sassendalen, Svalbard collected during 24 May – 2 June 2003. Values represent percentage frequency (\pm SE) for each species based on eight collections of droppings from both species (see text for details).

three samples). Whether the difference in colour represents above- (green) *vs* below-ground (brown) parts of *Equisetum* or different species (*E. variegatum* Schleich. or *E. arvense* L.) was undetermined. However, in either case, it is clear that the two goose species were selecting different items at the same time.

The first two PCA axes together accounted for 70.2% (38.7% and 31.5% respectively) of the variation in the data relating to faecal content. The first axis was characterised by high positive loadings of roots and high negative loadings of moss (Table 1), which effectively separated droppings of barnacle and pink-footed geese (Fig. 2). The second axis reflected the positive influence of graminoids and the negative influence of *Equisetum*, which varied in the droppings of both species and may simply reflect patterns of local abundance. Although sample sizes were small, they gave little sign of differences in diet between droppings collected from allopatric *versus* sympatric feeding geese. The high pink-footed goose value at the top of the ordination in Fig. 2 resulted from large numbers of graminoid epidermal fragments in that sample.

Discussion

To predict future patterns of distribution and abundance, it is essential to understand the nature of interactions between organisms competing for resources (either through depletion or interference). Aerodynamic constraints on the digestive system of long distance migratory avian herbivores restrict food digestion efficiency, compensated by their small size and ability to select specific plant parts high in nutrient content and/or energy. Many herbivorous waterfowl gather in large flocks to feed in rich habitats, so the potential for inter-, as well as intra-specific interactions is high. Despite this, competition between avian herbivores remains rarely studied, not least because distribution patterns in time and space of overlapping species

Table 1. Major plant groups identified in faecal material present in barnacle and pink-footed geese droppings in pre-breeding feeding areas during May 2003 and used to summarise differences in diet between the collections. Variables are ranked according to their loadings on PCA axis 1, showing eigenvalues for both of the first two axes.

Plant species/group	Eigenvectors axis 1	Eigenvectors axis 2
<i>Bistorta/Oxyria</i> rhizomes	0.539	-0.163
Unidentified below-ground tissue	0.489	-0.294
Unidentified epidermis	0.261	0.362
Graminoids	0.036	0.564
<i>Equisetum</i>	-0.191	-0.380
Dicotyledonous species	-0.256	0.418
<i>Salix</i> buds	-0.325	-0.205
Moss	-0.440	-0.169

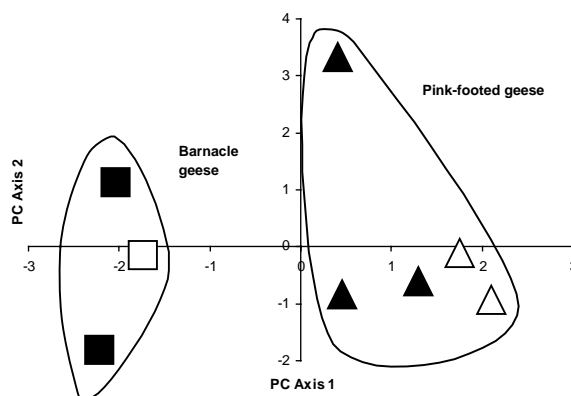


Fig. 2. Principal components analysis ordination of the content of collections of faeces collected from barnacle (squares) and pink-footed geese (triangles) using the pre-nesting feeding area at the mouth of Brattliddalen, Sassendalen, Svalbard collected during 24 May–2 June 2003. Samples are distinguished between those collected in allopatric situations at the time of observation (open symbols) and sympatric (filled symbols) for both species. The percentage of variation explained by these first two axes was 70.2% and the loadings of the different plant constituents present in the droppings are given in Table 1.

exploiting a feeding resource are frequently shaped by the very interaction that is the subject of study. Although Kristiansen and Jarrett (2002) demonstrated interference between two goose species during wing moult, exploitative competition seems to be more common. In seven studies of interactions between species pairs of non-breeding waterbirds, habitat selection was primarily affected by resource depletion, demonstrated through descriptive analyses or modelling (van Eerden 1984, Madsen 1985, 1988, Lorenzen and Madsen 1985, Madsen and Mortensen 1987, Fox 1996, Percival et al. 1996), also confirmed by manipulative experimentation (Sutherland and Allport 1994). In order to establish the potential for such interactions, an understanding of the degree of overlap in feeding behaviour, methods and diet is therefore an important prerequisite.

Migratory geese arrive in spring with depleted body stores to encounter a Svalbard landscape offering little higher plant growth. Earliest habitats exposed from snow tend to be the least productive, being the most free-draining affected by drought later in summer. Most productive plant communities are last to thaw, enabling accumulation of organic materials and improved productivity much later in the season (Prop and de Vries 1993). Despite this, shortly after arrival to the breeding grounds, females must have attained sufficient stores to lay a clutch of eggs, rich in lipids, protein and calcium, which in both species equates to c. 25% of female body mass (Appendices I and II in Owen 1980). Given competition between the same two species during the flightless moult in east Greenland (Madsen and Mortensen 1987), it was expected that the limited availability of food on arrival in Svalbard would be the

cause of inter-specific interactions during pre-nesting as well.

These results showed no dietary overlap in the two goose species during the prelude to first egg laying in Sassendalen during 2003, despite sharing similar diurnal feeding patterns, and spending similar amounts of time gathering food in the same restricted area. Pink-footed geese predominantly exploited over-wintering plant storage organs by grubbing into the upper 2–8 cm of the soil horizons, mostly the stout rhizomes of *Bistorta viviparum*, and below-ground parts of *Equisetum* spp. taken in more heathy communities. *Salix polaris* roots may also have been taken (based on visual observations) but were not found in droppings. Pink-footed geese also took *Dupontia* spp., *Alopecurus* spp. and other graminoids in moss-mat vegetation. Visual observations suggested that very little removal of above-ground plant parts occurred at this time, confirmed by the dominance of below-ground parts and abundance of soil particles in faecal material. Pink-footed geese were generalist foragers, exploiting all snow free habitat types by grubbing. Its larger body size, stouter bill and more robust neck musculature enabled more effective exploitation of below-ground parts than possible by the smaller, slighter barnacle goose.

In contrast, barnacle geese fed predominantly upon plant above-ground parts, well over 60% of which comprised moss (as found elsewhere, Prop et al. 1980, Prop and de Vries 1993), explaining their heavy use of moss-mat areas compared to other habitats. Barnacle geese took *Equisetum* and *Salix polaris* buds, derived from the drier, more free-draining, communities used at lower frequencies. Diet composition confirmed visual observations that this species forages most on above soil plant parts, completely removing the upper levels of moss mats locally. Perhaps because of high depletion rates, barnacle geese foraged most on the very edges of snow patches, although there was no evidence to suggest that this was due to higher plant growth initiated under the protective cover of snow as reported elsewhere (Fox et al. 1991). Visual examination found no production of above-ground green material amongst higher plants under the protection of snow in Sassendalen in May 2003. Rather, the species appeared to exploit newly exposed moss, *Equisetum* spp. or higher plants yet to break dormancy, i.e. responding to patterns of physical food availability, rather than food quality, as vegetation was exposed from under snow.

Only three inter-specific interactions were witnessed during 66 hours of intensive observations and further casual observations during the study, suggesting little evidence for aggression as a basis for competitive interference between the two species, although mutual avoidance would form the basis for segregation without overt signs of agonistic interactions. In fact, both species

fed in close proximity to each other without any indication of such avoidance.

We conclude that there was little, if any, food competition in Sassendalen (where the two species have co-existed for at least 50 years; Løvenskiold 1963) at observed goose densities, despite the potential for such interactions, and no indication that the two species avoided each other in time or space. Rather, the evolution of physical differences between the species has enabled the efficient exploitation of below-ground parts by the more robust pink-footed goose and that of above-ground parts by the smaller barnacle goose with its slighter bill. The resulting difference in diet effectively precludes exploitative competition between the two species. As long as goose densities have no long-term effects on the vegetation composition, further increases in goose numbers would have no inter-specific effects because of the lack of overlap in diets of the two species. In this case, only intra-specific density-dependent effects are likely to accrue with time. However, these results show that both species can exert extensive physical effects on the vegetation, i.e. pink-footed geese by their grubbing action, and barnacle geese by their physical removal of the growing tops of moss mat. If these physical effects have knock-on effects on plant composition, increases in one or other goose population may have inter-specific effects on the ability of the other to acquire nutrients in the prelude to reproduction, which may have fitness consequences (i.e. in terms of reduced reproductive success or survival).

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