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The feeding ecology of Greenland white-fronted geese Anser albifrons flavirostris was studied during spring staging in Iceland 1997. Geese feeding on Poa pratense dominated hayfields (> 80% cover) were highly selective, selecting for Deschampsia caespitosa which comprised only 10% of the sward. Geese fed most on the south-facing fringes of Deschampsia tussocks. Subsequent analysis showed that the southern fringes of Deschampsia tussocks supported significantly greater biomass (27% greater mass of green material) and that leaves growing on the southern faces had significantly higher protein content than those on the northern faces (33.9% vs 30.5%). It appears that the geese maximise their nutritional intake in spring by selecting the grass species of highest quality and taking the most nutritious parts of the plants.

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Arctic-nesting geese are relatively large herbivorous birds which undertake long distance migrations between breeding and wintering areas. Geese are highly selective when feeding, choosing the plant species and organs with the highest digestibility and nutrient content (e.g. Boudewijn 1984, Madsen and Mortensen 1985, Fox 1993). Geese face particular nutritional demands during the prelude to migration and breeding, when acquisition of stores of energy (to meet flight costs and reproductive demands) and nutrients (for investment by the female in reproduction) are more acute than other stages of their life cycle (Owen 1980, Krapu and Reinecke 1992).

Grass forms a major source of food for many northern goose species in spring, yet not all grass species exhibit the same nutrient content, nor share similar growth phenology, especially in northern latitudes where low ground temperatures restrict spring growth

early in the season. Fox (1993) showed that where *Phleum pratense* was the dominant grass in reseeded hayfields in Iceland, pink-footed geese *Anser brachyrhynchus* fed mainly upon this, the species with the highest protein and low crude fibre content. The same study demonstrated that over the course of four or more years, the *Phleum pratense* component of the sward declined rapidly, as native grasses (especially *Poa pratense* and *Deschampsia caespitosa*) invaded the hayfields and gradually dominated the sward. Little or no *Phleum pratense* is present in many hayfields in Iceland that are exploited by geese. What do these geese feed on there and how do they optimise their intake of other species of grass, to maximise nutrient acquisition?

Here we report a study of spring staging Greenland white-fronted geese *Anser albifrons flavirostris* in western Iceland, where birds stop for about three weeks en route to breeding areas in west Greenland from their

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wintering areas in Ireland and Britain. Staging geese accumulate stores in Iceland in preparation for their onward migration across the Denmark Strait and the Greenland ice-cap to ultimate summering areas (Anonymous 1997). The present study describes the feeding selectivity of Greenland white-fronted geese on hayfield swards and the exploitation of microtopographical features by the geese to maximise their intake.

Study site

The study was carried out at Hvanneyri Agricultural College in Borgafjördur, south-west Iceland (64°34'N, 21°46'W) during 16 April-9 May 1997. The area is a well known spring staging site for Greenland whitefronted geese (Francis and Fox 1987, Fox et al. 1994), comprising some 85 ha of relatively undisturbed hayfields (the college is a hunting free area) in close proximity to safe roost sites. About 90 fields were available to the geese within the Hvanneyri area, with Poa pratense, Agrostis sp. and Deschampsia caespitosa predominant. Phleum pratense was the dominant grass in only five of the fields and the majority of feeding geese exploited fields with little or no Phleum pratense in the sward. Intensive fieldwork for the present study took place on field no. 39, a 2.47 ha field which comprised mainly Poa/Deschampsia used by up to 94 white-fronted geese at any one time in the spring of 1997. On two occasions (5 and 8 May) two and five barnacle geese Branta leucopsis respectively were seen together with the white-fronted geese. No other herbivores were seen during the study period.

Methods

Sward composition

The sward composition in the field was sampled by recording the presence and percentage cover of all higher plant species in 25 randomly placed 10×10 cm quadrats. Mean percentage cover was calculated from all quadrats to give relative frequency of occurrence for each species.

Diet

Twenty fresh droppings were collected randomly from the site, preserved in 70% ethanol and thoroughly mixed before being microscopically analysed following the procedure of Owen (1975). To identify plant fragments, reference slides were made from the plant species identified in the field. The relative frequencies of plant fragments were determined by sampling 100 random points on each of ten microscope slides. We

compared species occurrence in the diet (d) with its frequency in the field (f) using Jacobs' index, D (Jacobs 1974) to give an index of selectivity: D = (f - d)/(f + d - 2fd). The index ranges from -1 (complete avoidance) to +1 (exclusive selection).

Tussock grazing

Once it was recognised the geese selected for *D. caespitosa*, thirty tussocks of this species were chosen randomly within the field (mean diameter 39.5 cm \pm SE = 1.02). From each tussock the number of leaves (grazed and ungrazed) were counted in a 3×3 cm square on the northern and southern quadrants of the tussocks (i.e. 45° either side of these cardinal points) and the proportion of grazed leaves recorded.

Nutrient content

From ungrazed tussocks green plant material was sampled from northern and southern sides and the outer (ca 2 cm) tips of fresh leaves (corresponding to the part taken by the geese) analysed for nitrogen content using a NA 1500 nitrogen analyser with leucin as standard. Crude protein was then measured by multiplying N-content by 6.25 (Hodgson 1983). The protein content was expressed as percentage of dry weight.

Results

Sward composition and diet

Comparison of plant frequencies in the droppings with those in the sward shows that the geese selected *D. caespitosa* and *Phleum pratense* (Fig. 1). *Poa pratense*, the most abundant species (ca 80% cover) on the field, was avoided despite comprising 50% of material in the droppings. *Alopecurus* sp., *Agrostris* sp. and *Ranunculus* sp. were all almost completely avoided.

Differences in shoot density

There were significantly more *D. caespitosa* (27%) leaves on the southern faces of tussocks (mean 33.6 \pm 1.3 SE 3×3 cm⁻¹) than the northern faces (mean 26.5 \pm 0.96 SE 3×3 cm⁻¹) (pairwise comparison, t = 4.57, DF = 29, p < 0.001).

Nutrient content

Leaf tips on the south-facing parts of D. caespitosa tussocks had a significantly higher crude protein con-

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tent than those on the northern fringes (south mean $33.85\% \pm 1.48$ SE, north mean $30.54\% \pm 1.07$ SE, arcsine transformed data, pairwise comparison, t = 4.161, DF = 5, p < 0.01).

Tussock grazing

Geese fed more on the southern fringes of tussocks, $(79.03\% \pm 3.77~\text{SE}~\text{grazed})$ than on the northern fringes $(25.82\% \pm 5.19~\text{SE}~\text{grazed})$ (arcsine transformed data, pairwise comparison, t=8.466,~DF=29,~p<0.001).

Discussion

Fox (1993) showed that the grazing intensity of pinkfooted geese in Iceland during spring was highly correlated with shoot density of Phleum pratense and that this species had the highest protein content (together with D. caespitosa) of all hayfield grass species analysed including Poa sp. (Fox 1993). In the study field considered here, however, Phleum pratense was highly restricted. The white-fronted geese showed a high preference for D. caespitosa which made out ca 30% of the diet. Indeed, the leaf tips of D. caespitosa selected by geese in this study showed even higher levels of protein content than the Phleum pratense encountered in the earlier study. Poa pratense, the most abundant plant species in the sward, was actively avoided although the diet still contained ca 50% of this species and hence, still might be an important food source during spring fattening. It would appear that D. caespitosa offers food of sufficient quality in

Sward and diet composition *D Cyp./Junc. Festuca rubra □ % in droppings Ranunculus sp. -1 % in sward Agrostris sp -1 Alopecurus sp. Poa pratense 0.56 Deschampsia caespitosa 0.50 Phleum pratense 0 20 40 60 80 100 Percentage

Fig. 1. Percentage frequency of plant species present in droppings (open bars) and the sward (shaded) of field no. 39 at Hvanneyri, spring 1997. Bars indicate means \pm standard error SE. ^aD = Jacobs index value (see text) which ranges from +1 (exclusive selection) to -1 (complete avoidance). Cyp./Jun. = Cyperaceae/Juncaceae.

the absence of Phleum pratense which is, in any case, better forage than the abundant Poa pratense (Fox 1993). Of course a comparison between sward and diet could be biased if geese regularly moving between fields of different sward composition. However, our clear impression was that geese usually stayed several days on the same field and hence, droppings in this study most certainly were produced by geese from the study field. When exploiting D. caespitosa, the geese encounter a plant species that grows in tussocks rather than an open sward and which apparently shows asymmetry of growth in terms of both biomass and crude protein. The geese responded to this asymmetry in the tussocks by feeding more intensively on the southern fringes, avoiding the northern sides and in this way optimising their protein intake. Hence, it would appear that shifting from one tussock to the next after having grazed only the southern fringe is a strategy that represents a more profitable strategy than remaining to feed on the whole tussock. Exactly what causes this difference in biomass and quality was not investigated during the present work, but temperature differences between north and south on such small scale tussocks is a phenomenon known to result from the differential interception of solar radiation (Hansen 1973), while the prevailing northerly winds at the study site (unpubl.) may have contributed to such differences in this study. High temperatures will speed up the mineralisation in the soil and, hence, increase the availability of for example nitrogen to the plants (Russell 1973, Lewis 1986). However, leaf growth, of course, is also highly dependent on light intensity (Holmes 1980). Early in the growing season, the low angle of incident solar radiation probably resulted in greater light intensities on the southern fringes of the tussocks (creating higher temperatures and better conditions for photosynthesis) than on the northern faces. Fox (1993) showed how geese selected swards at the field level, but not on a smaller scale within fields. This study confirms the ability of geese also to make fine-grained foraging choices to maximise nutrient intake by selecting between different species of food and by exploiting differences in forage quality resulting from microtopographic features affecting growth.

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