Food selection by barnacle geese (*Branta leucopsis*) in an Arctic pre-breeding area

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Keywords
Dietary analysis; food preferences; grass tiller size; interactions; moss; plant–herbivore; stopover ecology.

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doi:10.1111/j.1751-8369.2010.00172.x

Abstract

Detailed patterns of food selection by pre-breeding barnacle geese (*Branta leucopsis*) were investigated in Vårsolbukta, western Spitsbergen, Svalbard, in moss-dominated vegetation. This habitat is favoured by geese during the early Arctic spring when grass abundance is low. Grass is more profitable food than moss in terms of nutrient content and digestibility, and a five-fold higher proportion of grass in geese faeces compared with other vegetation indicated that geese selected grass in spite of its low availability compared with moss. As profitability may also depend on various properties that enhance searching efficiency, we studied the effects of grass tiller size, density and patchiness on goose selectivity in an experiment comparing ungrazed vegetation with vegetation where geese were allowed to feed for controlled periods of time. Large (two-leaved) tillers provided more biomass than small (one-leaved) tillers. The abundance of ungrazed large tillers relative to small tillers was lower in the grazed plots than in the ungrazed control plots, indicating that the geese preferred large tillers. Grass tiller density or spatial tiller distribution did not affect the degree of selectivity of geese for grass. Thus, we suggest that the feeding strategy of the geese in the early Arctic spring is primarily driven by the degree of tiller conspicuousness, as determined by tiller size. Furthermore, we suggest that an intense time allocation to feeding and an enhanced quality of grasses compared with mosses enabled geese to profit from feeding on the scarce grasses.

Herbivores with limited digestive capability, like geese (Owen 1980), usually exhibit selective feeding behaviour in order to forage optimally (Demment & van Soest 1985). They compensate their ineffective digestion by choosing food items of high quality that provide the maximal intake of nitrogen and energy (Black et al. 2007). However, it is not always favourable to select high-quality food items (Parsons et al. 1994; Thornley et al. 1994). The smaller or more cryptic a food item is, the longer is the search time (Gendron & Staddon 1983; Spaethe et al. 2001; Jones et al. 2006), which decreases the profitability of the food item. On the other hand, search efficiency, and consequently the profitability of the preferred food item, increases with density (Norberg 1977; Parsons et al. 1994) and aggregated distribution (Wallis de Vries 1996; Dumont et al. 2002).

In most Arctic habitats, moss is an important component of the vegetation, and its biomass often exceeds the biomass of more favourable food items such as grasses (Longton 1997; Born & Böcher 2001; van der Wal et al. 2001). This difference is even more pronounced during early spring, when mosses are available immediately after snowmelt and grass growth is still limited (Prop & de Vries 1993). However, young grass leaves contain more nutrients and are of better digestibility than mosses (Chapin et al. 1980; Prop and Vulink 1992; Hübner 2007), and consequently are more attractive for herbivores. This results in a trade-off situation for migrating geese in the early Arctic spring as they need to choose between an abundant low-quality food source and a much less abundant high-quality food source.

Arctic breeding geese, like the barnacle goose (*Branta leucopsis*), use pre-breeding stopover sites at high latitudes

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as stepping stones between their temperate staging areas and final breeding location in the Arctic (Arzel et al. 2006; Glahder et al. 2006; Hübner 2006). The use of stopover sites potentially enables them to adjust their arrival time at breeding sites and to build up body-fat reserves between the migration flight and breeding (Hübner 2006). Therefore, the stopover ecology of geese is important for our understanding of their breeding success and population ecology. However, no studies have been conducted on the feeding ecology of geese at Arctic spring stopover sites, and it is not understood how they accomplish reserve supplementation in these poor feeding conditions.

This study aimed to describe the current vegetation characteristics of the favoured feeding habitat in an Arctic pre-breeding stopover site for barnacle geese, and to determine the feeding strategy adopted by the geese. We hypothesized that the geese should select high-quality food, such as grasses, as long as this strategy is profitable, i.e., the nutritional gain exceeds the costs of obtaining the preferred food items. Grass tiller properties, which may influence the profitability of selective grass feeding, include size (Hassal et al. 2001; Bos et al. 2005), density (van der Graaf, Coehoorn et al. 2006) and detectability (Kristiansen et al. 2000), which includes the degree of aggregated growth (Wallis de Vries 1996; Dumont et al. 2002). We therefore predicted that during pre-breeding in the Arctic, geese (1) select for grasses and (2) prefer large tillers over small tillers. Also, we predicted their selectivity for grasses to be more pronounced when (3) the grass availability, i.e., tiller density, and (4) grass patchiness increase.

Prediction 1 was tested by comparing the diet composition of barnacle geese with the available plant biomass. To study the effects of grass tiller size (prediction 2), density (prediction 3) and spatial aggregation (prediction 4) the consumption of grass tillers by geese feeding in experimental plots was recorded. Furthermore, characteristics of the current vegetation were described.

Methods

Research area

Fieldwork was conducted in Vårsolbukta (77°45′N, 14°24′E), on the west coast of Spitsbergen, Svalbard, in spring 2005. Vårsolbukta is one of the few identified pre-breeding areas for geese in Svalbard (Mehlum 1998), and approximately one-fifth of the Svalbard barnacle goose population utilizes the area as a stopover site during spring migration (Hübner 2006). The first barnacle geese arrive in mid-May, and by mid-June most of the geese have left for their nesting locations (Prop et al. 1984; Hübner 2006, 2007). On average, individual geese spend less than four days in the area (Hübner 2006, 2007).

The habitat in which most geese in Vårsolbukta feed consists of a wet moss-dominated vegetation type, located below a bird cliff. The main plant species in this habitat are the moss *Calliergon richardsonii* and a variety of grasses. Early in spring, the dominant grass species that emerges is *Dupontia fisheri*. Other important vascular plant species are the grass *Arctophila fulva* and the dicot *Ranunculus hyperboreus*, but their availability is low during the time of the goose stopover. In this study we focused on the preferred vegetation type, which will be referred to as the *Calliergon–Dupontia* habitat.

Diet analysis

To assess the preferences of geese for different plant groups, we compared the proportion of food items in the goose diet with their proportion in the vegetation (prediction 1). Faeces of individual geese ($N = 25$) that had been feeding in the *Calliergon–Dupontia* habitat for at least 1 hour were collected between 19 May and 3 June. The geese were observed by telescope, and their faeces were relocated with the help of a drawing and another person. The faeces were dried, and then later re-dried in the lab at 50°C for 72 h and ground with 3 mm mesh size. In order to estimate the abundance of food items in the diet, between four and six subsamples of each faeces were inspected under a microscope (40×). Epidermis fragments of three plant groups (mosses, grasses and dicots) were recorded along a grid with 2 mm steps until 50 fragments were identified. This method is a common technique applied in several diet studies in geese (e.g., Prop & Vulink 1992; Stahl & Loonen 1998; Carriére 2002; Markkola et al. 2003; Fox & Bergersen 2005; Fox et al. 2009), and is regarded as a reliable method.

To analyse the available food biomass for geese in the vegetation, we harvested the aboveground biomass of eight plots (10 × 20 cm) on 28 May. These plots were established randomly in the *Calliergon–Dupontia* habitat prior to goose arrival, allowing the geese free access. Sampling the biomass only once was adequate for estimating the available biomass of moss and grass for the period of dropping collection, as it does not change significantly during this time in the focal habitat (Hübner 2007). The samples were dried in the field and divided into the same plant groups as used for the faecal analyses. A colour code and reference samples were established to distinguish live moss from dead moss, and all plant groups were then sorted to living and dead. Finally, samples were re-dried at 50°C for 72 h and weighed.

Feeding strategy experiment

The effects of grass properties on the feeding strategy of the geese were studied in an exclosure experiment (predictions 2, 3 and 4). Sixteen plots (1 × 1 m) with an adjacent control plot (40 × 40 cm) were established in the *Calliergon–Dupontia* habitat before the arrival of the geese. The only other herbivore in the area is the Svalbard reindeer (*Rangifer tarandus platyrhynchus*). As the plots were established shortly after the area became snow-free, the probability that reindeer were grazing on them prior to the establishment of the exclosures is negligible. Both the experimental and the control plots were covered by exclosures to prevent uncontrolled grazing. To ensure similar vegetation in the control–experimental plot pairs, the proportion and distribution of grass cover (mainly dead leaves from the previous year) was determined visually.

The plot pairs were placed on snow-free vegetation between 9 and 14 May. Because of the limited extent of the snow-free area, and in order to be able to observe multiple plots simultaneously, the plot pairs were placed in three groups (two groups of five and one of six pairs), with the groups being spaced approximately 150–200 m apart. Within the groups, the plot pairs were randomly distributed with a distance of 5–40 m between them. Corners of the experimental plots were marked with small pegs, allowing the observer to draw imaginary plot boundaries.

The groups of experimental plots were opened for controlled goose grazing, all plots within a group simultaneously, on 31 May, and 1 and 2 June, respectively. With the help of a telescope, the number of geese in each plot was recorded at 1-minute intervals, with the sum of all recorded geese in a plot producing an estimate of grazing time (goose min/m^2). This was included as a covariate in the statistical analysis.

However, because of adverse weather conditions, the moss layer was partly frozen, and standardized moss sampling was not possible. Hence, the grass/moss ratio could not be calculated. The variable grazing time is accounted for by including this variable as a covariate in our analyses of grass selectivity.

Immediately after the grazing trials, nine and four evenly distributed cores (9.4 cm in diameter) were taken from the experimental and the ungrazed control plots, respectively. The cores contained all live aboveground material of the grasses within the circle.

To measure the grass availability in terms of density, the tillers were counted in each core. The relationship between tiller density and available grass biomass was studied by using the tiller counts of control cores. Grass biomass within plots was determined by pooling grass material from all cores, following the same procedure as described for the biomass analyses in the diet analysis (see above).

A measure of grass tiller consumption by the geese was achieved by tiller counts of the experimental plots, recording whether the tillers were grazed or not. As microtines are absent from the area, and no larger herbivores visited the plots during the experiment, all grazed tillers were consumed by the geese.

To study the effect of grass tiller size on selectivity, the ungrazed tillers in all cores were further categorized into small and large tillers. Tillers with only one leaf, in most of the cases grown during the current spring ("young leaf"), were defined to be small tillers. Tillers with two leaves were defined as large tillers. In addition to the young leaf they had an older leaf ("old leaf"), which in most cases had overwintered and therefore had a dead tip (<0.5 cm). None of the tillers had more than two living leaves.

To study the relationship between tiller density and weight, the tiller weights for small and large tillers were estimated by measuring the weights of the two leaf types (young and old). In one randomly chosen core of each control plot, all living leaves were picked. Subsequently, the dry weight of young and old leaves was measured separately, following the same procedures as for the biomass analyses.

Calculations and statistical methods

All statistical analyses were performed using the software package R v2.7.2 (R Development Core Team 2008). Results are given as means ± SEs, unless otherwise stated. The sampled grass biomass and the grass tiller numbers per plot were extrapolated to total quantities per square metre prior to the analyses.

Tiller weights (mg/tiller) for small and large tillers were established from the leaf weights (mg/leaf). The mean weight of young leaves was used as an estimate for small tiller weight, and the sum of the mean weights of the young and old leaves was used as an estimate for the large tillers. To study the effect of tiller density (tillers/m^2) and spatial distribution of tillers (the variance of tiller numbers between cores within a plot) on the total biomass of grasses (g/m^2) and the weight of individual tillers, linear regression models were fitted to the data. To normalize the data, log-tranformed variables were used for this analysis. The Akaike information criterion for small sample sizes (AICc; Burnham & Anderson 2002) was used to select the most appropriate model.

Proportions of food items in goose faeces and in the vegetation were compared using a multivariate analysis of variance (MANOVA, with Pillai trace). As the

Table 1 Model selection (linear regression) for total grass biomass, weight of large tillers (= Wlarge) and small tillers (= Wsmall) in ungrazed *Calliergon–Dupontia* vegetation in Vårsolbukta, Svalbard, spring 2005. Predictor variables: density = log (tillers/m^2); distribution = log (variance of tillers/core). Variables included in the models are indicated with a "×". The models are ranked according to the corrected Akaike's information criterion (AICc).

Response variable	Density	Distribution	Np[a]	AICc[b]	ΔAICc[c]	AW[d]
Log biomass g/m^2			**0**	**33.92**	**0**	**0.45**
		×	1	34.48	0.55	0.34
	×		1	36.33	2.41	0.13
	×	×	2	37.65	3.73	0.07
Log Wlarge (mg)	**×**		**1**	**13.07**	**0**	**0.76**
	×	×	2	16.25	3.18	0.16
			0	18.28	0.07	0.06
		×	1	19.88	6.82	0.03
Log Wsmall (mg)	**×**		**1**	**15.18**	**0**	**0.55**
			0	17.04	1.85	0.22
	×	×	2	18.23	3.04	0.12
		×	1	18.40	3.22	0.11

[a] Number of parameters in the model.

[b] Corrected Akaike's information criterion.

[c] Difference in AICc between the present model and the best model.

[d] Akaike weight.

percentage of one food item was dependent on the percentage of the other food items in the sample, the data were log-ratio transformed to achieve linear independency (Aebischer et al. 1993). To avoid zero values in the data, 0.01 was added to all values prior to the transformation. This value was chosen because it was an order of magnitude smaller than the smallest values of the data set, as recommended by Aebischer et al. (1993).

To study grass tiller size preference, the difference in the small tillers/large tillers ratio between control and experimental plots was tested with a paired Student's *t*-test.

The grass consumption rate was measured as the proportion of grazed tillers to all tillers. An AICc selected binomial logistic regression was used to evaluate the effects of grass tiller density and spatial distribution (within-plot variance in density) on tiller consumption. Correlations between the tiller densities (total, small and large tillers) and spatial distribution of tillers were evaluated with the Pearson's product–moment correlation.

Results

Characteristics of ungrazed vegetation

Moss constituted the major component of vegetation available for the geese in our study area (237.3 ± 27.0 g/m^2), with grasses (7.0 ± 0.9 g/m^2) and dicots (1.7 ± 0.5 g/m^2) representing only a small fraction.

In the ungrazed control plots, the total tiller density was 3880 ± 450 tillers/m^2. The within-plot variance of tiller numbers per core was 105.6 ± 31.0 (range: 8–483). Thus, the spatial distribution within plots showed a wide range of different degrees of patchiness. The density and variance did not, however, explain the difference of total grass biomass between these plots (10.0 ± 1.8 g/m^2), which was best explained by a null model (linear regression, coefficient = 2.1; 95% confidence interval, CI = 1.7–2.5; Table 1).

Young leaves weighed on average 0.8 ± 0.1 mg, whereas old leaves were significantly heavier (1.3 ± 0.8 mg; paired Student's *t*-test, difference = 0.5 mg; 95% CI = 0.2–0.8). The biomass of large tillers (2.1 ± 0.2 mg) was therefore on average 2.8 times the biomass of small tillers (paired Student's *t*-test, difference = 1.3 mg; 95% CI = 0.9–1.7).

The majority of tillers were small, their density being 2920 ± 350 tillers/m^2, whereas the density of large tillers was 710 ± 107 tillers/m^2. The weight of large tillers was best explained by tiller density alone (tillers/m^2) (linear regression, Pearson correlation coefficient, $r_P = -0.6$; coefficient = –0.6; 95% CI = –1.0 to –0.2), with the tiller weight decreasing with increasing density (Fig. 1; Table 1). The same was true for small tillers, even if the decrease was weaker and more uncertain (linear regression, $r_P = -0.5$; coefficient = –0.4; 95% CI = –0.9 to 0.003) (Fig. 1; Table 1). This indicates that the most profitable tillers, in terms of size, are found where tiller densities are relatively low.

Selection between plant groups

Mosses formed the main food item group in the diet of the geese (Table 2). However, the proportion of grass in the goose faeces was almost five times higher than in the

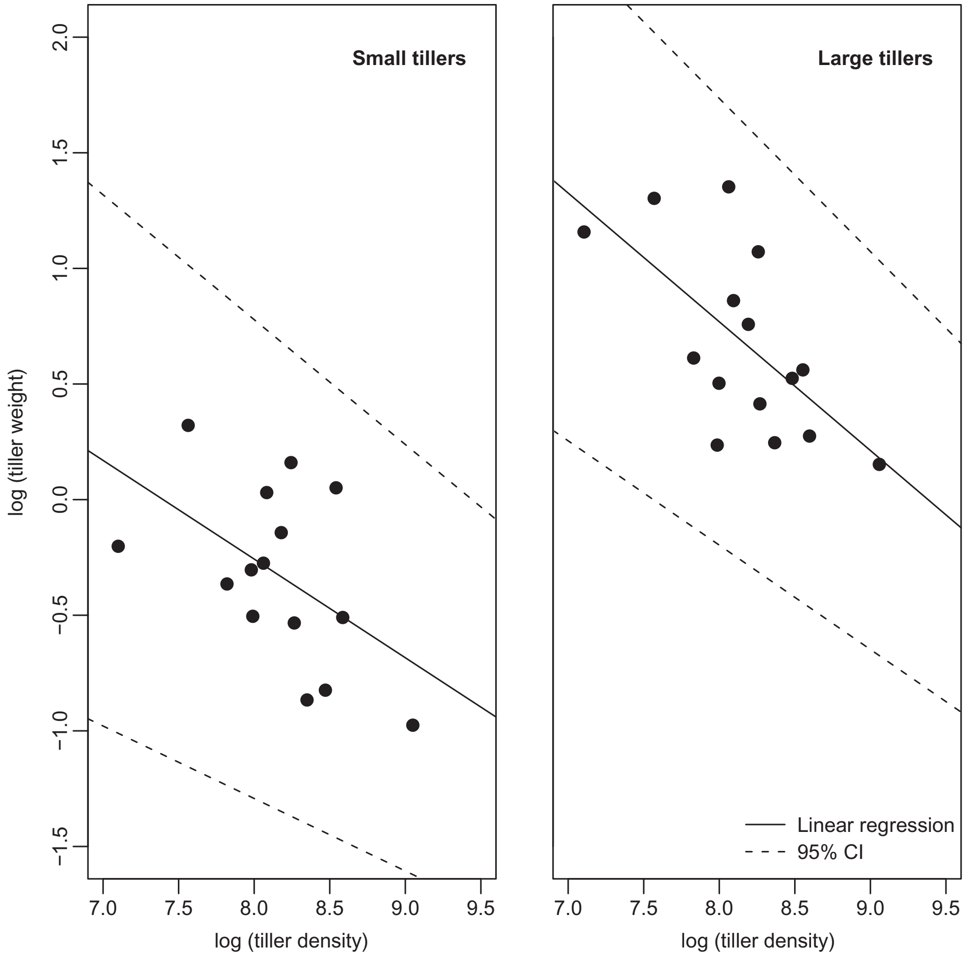

Fig. 1 The relationship of tiller density (tillers/m^2) and tiller weight (mg/tiller) for tillers with one leaf (small tillers) and two leaves (large tillers), respectively, in ungrazed vegetation in the *Calliergon–Dupontia* habitat in Vårsolbukta, Svalbard, spring 2005. Linear regression lines and 95% confidence intervals (CIs) are shown.

Table 2 Mean percentages ± SEs of food items in the *Calliergon–Dupontia* habitat and in the faeces of barnacle geese during a prebreeding stopover in Vårsolbukta, Svalbard, spring 2005.

Food item	Habitat ($N = 8$)	Faeces ($N = 25$)
Moss	96.1 ± 0.01	81.9 ± 0.03
Grass	3.2 ± 0.01	15.7 ± 0.03
Dicot	0.7 ± 0.00	2.4 ± 0.01

vegetation, indicating that the geese selected for grasses (MANOVA, $F_{1,31} = 4.6$, $P = 0.02$; Table 2).

Grass tiller grazing

Geese grazed on average 16 ± 0.02% of tillers in the experimental plots.

The ratio of ungrazed small to ungrazed large tillers was significantly higher in the experimental plots (8.6 ± 1.3) than in the control plots (5.2 ± 0.9, paired Student's *t*-test with log-transformed data; difference = 0.5; 95% CI = 0.3–4.7). This lower relative density of large tillers in the grazed vegetation indicates that they were grazed more often than the small tillers.

Grass consumption by the geese was best explained by a null model (binomial logistic regression, intercept = −1.69, $P = 0.02$; Table 3). Removing an outlier with the lowest consumption, which originated from the plot where geese fed for the shortest period (11 min), did not change these results. Thus, factors other than grass tiller density and spatial variation seem to be more important for the grazing pattern of geese.

However, density and within-plot variance for the total tiller densities were strongly correlated in experimental plots ($r_P = 0.83$, $P < 0.001$; for control plots $r_P = 0.42$, $P = 0.1$), so the independent effects of density and degree of tiller patchiness was difficult to separate. This was also

Table 3 Model selection (logistic binomial regression) for grass consumption (= grazed tillers/all tillers) by barnacle geese in the *Calliergon–Dupontia* habitat during a pre-breeding stopover in Vårsolbukta, Svalbard, spring 2005. Predictor variables: density = log(tillers/m^2); distribution = log(variance of tillers/core); time = grazing time of geese in plot (min). Variables included in the models are indicated with a "×". The models are ranked according to the corrected Akaike's information criterion (AICc).

Response variable	Density	Distribution	Time	Np^{a}	AICc^{b}	ΔAICc^{c}	AW^{d}
Consumption				**0**	**7.38**	**0**	**0.52**
	×			1	10.09	2.79	0.13
			×	1	10.09	2.71	0.13
		×		1	10.10	2.73	0.13
	×	×		2	13.28	5.91	0.03
		×	×	2	13.29	5.91	0.03
	×		×	2	13.29	5.90	0.03
	×	×	×	3	17.11	9.73	0.00

[a] Number of parameters in the model.

[b] Corrected Akaike's information criterion.

[c] Difference in AICc between the present model and the best model.

[d] Akaike weight.

true for small tillers in control plots ($r_P = 0.49$, $P = 0.06$), but not for large tillers ($r_P = 0.19$, $P = 0.49$).

Discussion

To our knowledge this is the first study to investigate grass selection patterns of geese in the High-Arctic spring. In spite of the low availability of grasses in the vegetation during that period, the geese were selectively feeding on grasses (fulfilling prediction 1), even if moss formed the major part of their diet. They preferred large grass tillers above small ones (in keeping with prediction 2). The selectivity of the geese for grass was neither affected by tiller density nor patchiness (so predictions 3 and 4 were not fulfilled). Thus, factors other than tiller distribution seemed to be important for the grazing pattern of the geese.

Selective foraging in patchy environments

Body condition before breeding is an important factor in determining the reproductive success of Arctic breeding geese (Ebbinge & Spaans 1995; Prop & Black 1998; Drent et al. 2003). Feeding conditions in the Arctic are poor during pre-breeding because the energy-rich food sources, such as grass leaves, are still small and scarce after the winter; whereas access to moss is only limited by snow cover (Prop & de Vries 1993; Hübner 2007).

Because the digestive tract of geese is inefficient (Owen 1980), the most profitable feeding strategy would be—all things being equal—to select the high-quality grass leaves and avoid moss because of its low nutrient content and digestibility (Chapin et al. 1980; Prop & Vulink 1992; Hübner 2007). However, feeding on less abundant food results in long searching times and a low food intake rate (Norberg 1977; Parsons et al. 1994). In this study, barnacle geese had an approximately five-fold higher proportion of grasses in their diet compared with the available vegetation. Thus, it is evident that the geese used a selective feeding strategy in spite of the low availability of good-quality food items in the vegetation (3% grass of the total live aboveground plant biomass). Even if the search time for grasses is likely to be longer than for moss, this does not seem to counteract their nutritional advantage. These results are in line with the study of Alsos et al. (1998), who found female barnacle geese selected grass even at low availabilities (5% of vegetation cover) during incubation.

A possible explanation for the selectivity of scarce food items is an enhanced nutritional difference between the available food sources. Grass quality is highest early in spring and decreases over the course of the growth season (Chapin et al. 1980; Crawley 1983; Manseau & Gauthier 1993; van der Graaf, Stahl et al. 2006). Similar changes in mosses have not been studied. During early spring, the difference in quality between vascular plants and mosses is nevertheless likely to be at its peak, presumably compensating for the low availability of grasses. Manure from seabirds has been found to increase the nutrient content of vascular plants growing below bird cliffs (Anderson & Polis 1999; Born & Böcher 2001). However, a comparable increase of nitrogen content could not be shown for mosses below the bird cliff in the present study area (Hübner 2007). Consequently, differential responses to seabird manure between grasses and mosses may enhance the quality difference between preferred and less preferred food items even further at this study site.

Detecting and selecting grasses in a moss carpet

Geese feeding on small grass tillers have a small bite size, resulting in low intake rates (Hassal et al. 2001). Consequently, geese should prefer larger tillers, which is also the case in the present study.

Tiller size difference in this study was based on the number of leaves, and a large tiller, with both a young and an old leaf, contained more than twice the volune of biomass than a small tiller. However, newly grown young leaves contain more nutrients and less structural components than old leaves from the previous year (Cargill & Jefferies 1984; Sedinger & Raveling 1986; Manseau & Gauthier 1993). Because of this lower quality, the additional old leaf in the large tiller probably only marginally adds to the quantity of nutrients in the tiller, in spite of the increased biomass. The difference in nutrient intake provided by small and large tillers is thus unlikely to determine their profitability alone.

An alternative explanation for the preference of geese for large tillers is their augmented conspicuousness (Kristiansen et al. 2000). The vegetation in the *Calliergon–Dupontia* habitat consisted of a thick moss layer interspersed with grass tillers. At the time of the goose stopover, many dead grass leaves were still attached to the tillers, and protected the living part that had barely emerged above the moss layer (mean length of leaves from 50 tillers of *D. fisheri* collected in the *Calliergon–Dupontia* habitat in the study area on 3 June 2003: 2.1 ± 0.1 cm and 3.1 ± 0.1 cm for young and old leaves, respectively). Under such conditions, large tillers are likely to be easier to detect for the geese than small ones, and selecting large tillers would thus enhance the search efficiency. In order to optimize their feeding, both in relation to search time and gain of nutrients, geese may select the young nutrient-rich leaves of large conspicuous tillers. The methods used in this study did not, however, allow for quantifying the relative consumption of leaf types in large tillers.

Conspicuousness of food plants may also be enhanced by patchy growth. Patchy resources have been found to increase the search efficiency of herbivores, and to thus favour selectivity over a range of densities and spatial scales (Edwards et al. 1994; Dumont et al. 2002). However, the effects of food item properties on foraging strategies are poorly understood (Jones et al. 2006). If searching efficiency is a significant component of the profitability of grass tillers, geese should show a higher degree of selectivity when tillers grow more clustered, but such a pattern was not found in this study. The density of small tillers correlated with the patchiness, whereas the density of large tillers did not. Consequently, the easier detectability of larger tillers may have counteracted the effect of tiller patchiness on the searching efficiency of the geese.

Grass tiller density did not seem to affect the degree of selectivity of the geese either. As the total tiller density and tiller patchiness were correlated, it was not possible to unravel their separate effects on tiller consumption by the geese. Furthermore, both small and large tillers decreased in weight when tiller density increased. The benefit of increased tiller density was therefore partly counteracted by a reduction in biomass per tiller. This is further supported by the findings that the total grass biomass in a plot was independent of the tiller density.

In summary, the geese in this study were feeding selectively on grasses in spite of the low availability. The geese preferred grasses with two leaves, which provided more biomass and were easier to detect. Such enhanced conspicuousness is an important feature when preferred food items are generally small, scattered and hidden within the surrounding vegetation. Furthermore, neither the overall tiller density, nor patchiness, were found to have an effect on their selectivity, which was probably because of the decreased weight and detectability of densely growing tillers. We therefore suggest that the conspicuousness of food items plays an important role in the food selection of geese during the early Arctic spring.

Acknowledgements

We thank Hanna Kokko, Markus Öst and Rosie Barlak for comments on an earlier version of the manuscript. We are grateful to Cecilia Sandström, Jannik Schultner and Joris Tinnemans for sorting some of our samples. We thank Nigel Gilles Yoccoz and Niels Felsted Thorsen for their help with the R statistical program, Rolf A. Ims and Jouke Prop for comments on the manuscript, and Ellen Kathrine Thomassen for help with the language. This study was financed by the Norwegian Research Council, the Roald Amundsen Centre for Arctic Research, in Tromsø, and the Norwegian National Committee on Polar Research. At the time the research reported here was carried out the authors were affiliated with the University Centre in Svalbard. EMS was also affiliated with the Department of Biological and Environmental Sciences of the University of Helsinki.

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