DOES SIZE MATTER? MAXIMISING NUTRIENT AND BIOMASS INTAKE BY SHOOT SIZE SELECTION AMONGST HERBIVOROUS GEESE

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The selectivity of Greenland White-fronted Geese *Anser albifrons flavirostris* feeding on Timothy *Phleum pratense* hayfields in Iceland during their spring staging was studied in three fields of different shoot density (high, medium and low) and discussed in the context of optimal foraging. Biomass and nitrogen content of the *Phleum* laminae (leaves) taken by the geese were analysed and correlated to lamina length. In all fields the geese were highly selective for the larger laminae, ignoring shorter ones. Because the quality (nitrogen content) of the laminae decreased only slightly with increasing lamina length, the geese maximised their intake per peck by only taking the largest laminae. This study suggests that, even at high peck rates, herbivorous geese are capable of selecting most profitable bite sizes at a fine grained scale.

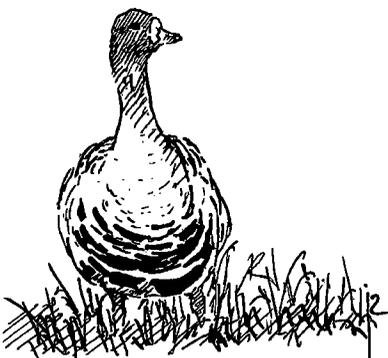Keywords: *Anser albifrons flavirostris - Phleum pratense* - nutrient & biomass intake

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INTRODUCTION

The way animals optimise or maximise their intake has been demonstrated empirically for several different predators (e.g. Davies 1977; Goss-Custard 1977a; Krebs *et al.* 1977; Sutherland 1982; Sutherland & Ens 1987; Ens & Alting 1996). These animals usually select according to prey size. However, animals do not only select prey according to size (biomass) but may also select for quality (energy or nutrients) such as high protein content (e.g. Moss *et al.* 1972; Goss-Custard 1977b, Fox *et al.* 1991; Fox 1993; Kristiansen *et al.* 1998). In contrast to carnivores, the diet of a herbivore is relatively low in nitrogen content and high in indigestible fibre content by virtue of the nature of their food plants (e.g. Crawley 1997). Thus, they must ingest relatively large amounts of plant material to derive sufficient energy and nutrients. Therefore, it must be advantageous to these animals to exhibit some degree of selectivity.

True geese (*Branta* and *Anser*) are herbivores that have relatively poor digestive systems and spend much of their time feeding (Owen 1980). These birds select plant species with highest nutrient and lowest fibre content (e.g. Boudewijn 1984; Madsen & Mortensen 1985), and select those plant parts of highest quality from those available (Fox 1993; Kristiansen *et al.* 1998; Therkildsen & Madsen 1999). However, the selected plant parts may also vary in both size and quality which further affect the profitability of particular parts. Our prediction would be that, faced with a range of food items, geese would maximise their intake

of material of highest quality. In this study we examine bite size and quality in Greenland White-fronted Geese *Anser albifrons flavirostris* feeding on Timothy *Phleum pratense* and discuss their selection in the context of selective foraging.

STUDY SITE AND METHODS

Greenland White-fronted Geese winter in Ireland and Scotland and migrate through Iceland where they stop over for about three weeks before continuing to their breeding areas in West Greenland. This study was conducted in 1999 on hayfields at Hvanneyri Agricultural College, West Iceland (64°34'N 21°46'W) one of the two main spring staging sites (Francis & Fox 1987; Fox *et al.* 1994; 1999). In Iceland the geese feed to gain sufficient energy and nutrients for the last part of the journey and contribute to subsequent breeding (Anonymous 1997; Boyd *et al.* 1998; T. Nyegaard *et al.* unpubl. data). During the first part of their stay in Iceland the geese feed predominantly on hayfields comprising *Phleum pratense* which is the only green biomass available at that time (T. Nyegaard *et al.* unpubl. data). Later, as other potential food plants start to grow, they also feed on other grass species such as Smooth Meadow-grass *Poa pratense* and Tufted Hair-grass *Deschampsia caespitosa* as well as on traditional Lyngbye's sedge *Carex lyngbyei* sedge meadows. When feeding on *Phleum* the geese select almost exclusively for the youngest middle lamina (here referred to as the a0-lamina) leaving the other laminae (i.e. the second youngest a1, third youngest a2 etc.; Fig 1.; Fox 1993).

Three fields were chosen for the study; one comprising high density of *Phleum* shoots (field 1: mean (± SE) 36.50 ± 3.83 shoots 100 cm^{-2}, based on counts from 25 randomly placed 100 cm^2 quadrats), one intermediate (field 2: 16.31 ± 1.44 shoots 100 cm^{-2}) and one comprising low density (field 3: 9.94 ± 1.14 shoots 100 cm^{-2}). To assess the size distribution of the a0 laminae of the *Phleum* shoots in each field a 100 cm^2 quadrat was placed randomly ten times in field 1 (24

April) and 15 times each in fields 2 (2 May) and 3 (2 May) and all shoots (both the eaten and the uneaten ones) were clipped to ground level and removed, 8 and 16 days after the arrival of the geese. Because grass sampling was done at night following a day of intense goose grazing, the laminae taken by the geese had freshly cut green surfaces and therefore only little or no regrowth was expected to have occurred. The length of lamina a0 for uneaten shoots was measured in millimetres. To assess the length of the a0 lamina of the eaten shoots, ungrazed *Phleum* shoots were measured and the length of the 'missing' a0 lamina was modelled using simple regression based upon the length of the a1 lamina (the second youngest leaf), assuming that the relationship between a1 and a0 laminae was the same for grazed and ungrazed laminae. To test for differences in size class distribution between all available laminae and those taken by the geese and between laminae taken by the geese with the largest available laminae we used Kolmogorov-Smirnov two-sample tests. The size classes selected by the geese (d) were also compared with the frequency in the fields (f) using Jacob's index, D (Jacobs 1974) to give an index of preference: $D = (d - f) / (d + f - 2df)$. The index ranges from –1 (complete avoidance) to +1 (exclusive preference). Since cosine(v), where $0 \leq v \leq \pi$, is a sigmoid function that takes values between –1 and 1, we used this function as a basis for transforming D, i.e. $D' = \cos^{-1}(D)$. Hence, D = -1 corresponds to $D' = \pi$, D = 0 to $D' = \pi/2$ and D = 1 to $D' = 0$. The transformed index values were applied as the dependent variable in an analysis of covariance (PROC GLM in SAS) using field as an independent qualitative (class) variable and lamina length as an independent quantitative covariate. Significant effects due to either fields or interactions between fields and lamina length were tested *a posteriori* by means of linear contrasts in order to identify pairwise differences between fields with respect to intercepts and slopes. To reduce the risk of type I errors in these tests, a sequential Bonferroni procedure was applied to test the individual hypotheses (Simes 1986; Hochberg 1988). If the number of

null-hypotheses to be tested is m, the associated P-values for each of these tests are ordered in ascending order, that is, $P_{(1)} \leq P_{(2)} \leq ..... \leq P_{(i)} \leq ... \leq P_{(m-1)} \leq P_{(m)}$. The ith null-hypothesis (H_{0i}) is rejected if the P-value associated with that particular hypothesis $(P_{(i)})$ meets the condition

$$P_{(i)} \leq \alpha' = \frac{\alpha}{m - i + 1}$$

where α is the level of significance used in a single test ($\alpha = 0.05$) and α' the level of significance used in the specific test. The analysis also yielded predicted values of D', which were back transformed by a cosine transformation. The predicted D' may take values outside the permitted range, but in such cases $D' < 0$ can be replaced by $D' = 0$ and $D' > \pi$ by $D' = \pi$.

The lengths of the a0 laminae were converted into biomass using the following formula: $DM = 1.55L - 0.27$, where DM = dry mass, mg and L = length, mm, of the a0 lamina, (Fox *et al.* 1998). As nitrogen, N (as an ingredient of protein) content is considered an index of quality, we measured the N-content of the following ungrazed a0 lamina size classes: 3-6, 7-9, 10-12, 13-15, 16-18, 19-21, 22-24, 25-27 and 28-30 mm. Each size class was analysed for N-content (% of dry mass) using a NA 1500 nitrogen analyser with BBOT $(C_{26}H_{26}N_2O_2S)$ as standard. For each size class 5-6 samples were analysed. The profitability of each length class was calculated as the total mg N intake bite^{-1}.

RESULTS

The best fit on the relationship between a1 and a0 lamina from ungrazed *Phleum* shoots was: a0 = 0.5372a1 - 0.1229 ($r = 0.75$, $n = 454$, $P < 0.0001$). Fig. 2 shows the frequency distribution of all available shoots and the estimated a0 *Phleum* size classes taken by the geese in each of the three fields. Field 1 (Fig. 2a, the high density field) comprised smaller laminae than the intermediate (Fig. 2b, field 2) and the low density fields (Fig.
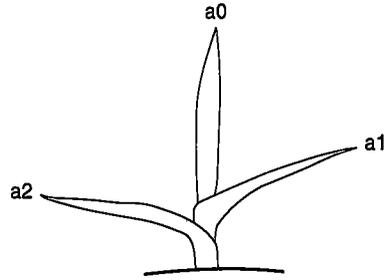

Fig. 1. Schematic illustration of a *Phleum pratense* shoot showing the youngest (middle) lamina a0, the second youngest lamina, a1 and the third youngest lamina a2.

2c, field 3). Geese selected a disproportionate fraction of the larger a0 lamina in all fields (Kolmogorov Smirnov Two-Sample Test, field 1: D_{max} = 0.473, $P < 0.001$, $n = 45$; field 2: D_{max} = 0.4, $P < 0.001$, $n = 58$; field 3: D_{max} = 0.473, $P < 0.001$, $n = 25$;). The geese selected exclusively the largest laminae in fields 3 and 2 (KS, field 3: D_{max} = 0.32, n.s., $n = 25$; field 2: D_{max} = 0.017, n.s., $n = 58$) but although the range of selected laminae in field 1 all were within the range of the larger laminae, they were significantly smaller than if the geese exclusively took the largest available (KS, field 1: D_{max} = 0.356, $P < 0.05$, $n = 45$). When the geese fed on the low and the intermediate shoot density fields, they took larger a0 laminae compared to the high density field. The probability that a lamina was taken increased with lamina size, all were taken above 26 mm in field 2 and above 25 mm in field 3.

Jacob's preference Index also showed that the geese avoided the smaller laminae and clearly selected for the larger ones (Fig. 3). There was an overall significant effect of lamina length and interaction between lamina length and field ($F_{5,77}$ = 42.25, $P < 0.0001$). The latter implies an overall significant difference among fields with respect to slopes. When the slopes of the fields were compared pairwise using linear contrasts the following results were obtained: Field 1 differed significantly from field 2 ($\alpha' = \alpha/3 = 0.0167$; $F_{1,77}$ = 11.15; $P_{(1)} = 0.0013$), whereas fields 1 and 3 ($\alpha' = $
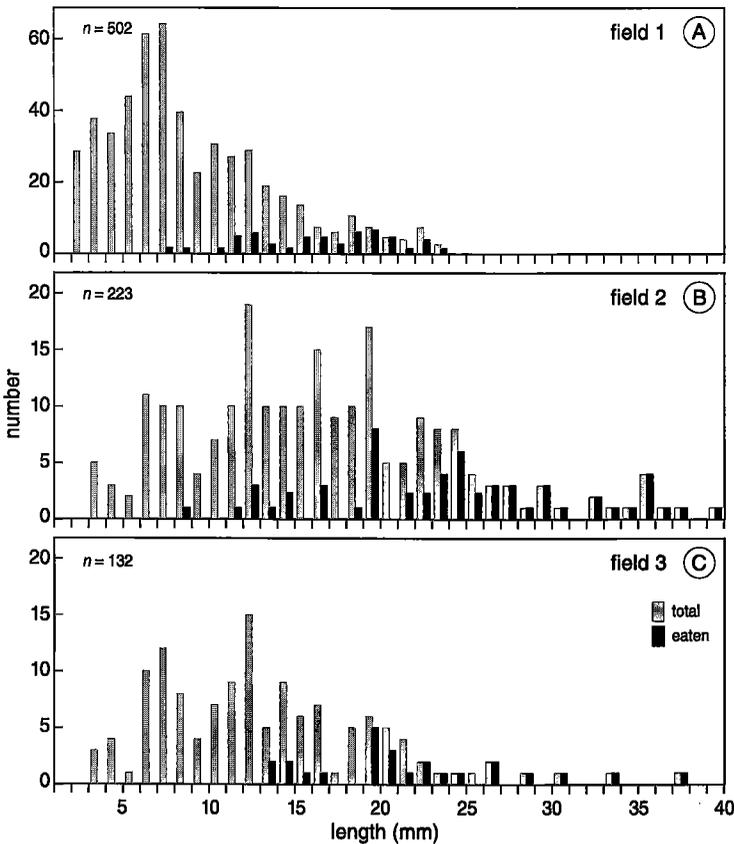
Fig. 2. Frequency distribution of *Phleum pratense* youngest lamina size classes available (shaded bars) in three Icelandic hayfields (A-C: field 1, field 2 and field 3) and the frequency distribution of the size classes taken by Greenland White-fronted Geese 1999 (black bars).

$\alpha/2 = 0.025$; $F_{1,77} = 4.13$; $P_{(2)} = 0.0457$) and fields 2 and 3 ($\alpha' = \alpha = 0.05$; $F_{1,77} = 2.66$; $P_{(3)} = 0.1069$) did not differ significantly. Field 1 (the high density field) showed the most marked shift from no selection to active selection followed by field 3 (the low density field) and field 2 (the medium density field). The selection thresholds (i.e. the inflection point at which $D = 0$) were 23.4 mm (field 2), 20.6 mm (field 3) and 13.7 mm (field 1). In all fields, above this critical threshold lamina length, selectivity remained constantly high (c. D = 0.6-0.8).

There was a slight but significant decline in N-content with increasing lamina length (Fig. 4). Relating N-content to biomass (lamina length) (based on biomass/lamina length-relationship (Fox *et al.* 1998) and using N-content from Fig. 4 this study) total N intake (milligrams per lamina)

increased with lamina length (Fig. 5). Hence, by selecting the larger laminae the geese gained both in terms of quantity and quality, per bite.

DISCUSSION

Optimal foraging theory assumes that the geese are able to distinguish between lamina of different quality and quantity (size) and that they select the best (Krebs & Davies 1978). The Icelandic spring staging geese not only select for *Phleum pratense*, the grass species with the highest N-content, (T. Nyegaard *et al.* unpubl. data) but also select for the part (i.e. the middle, youngest lamina, a0) of the plant with the highest nutrient value (Fox 1993). In addition, the present study has shown that geese are able to exploit and select on an even
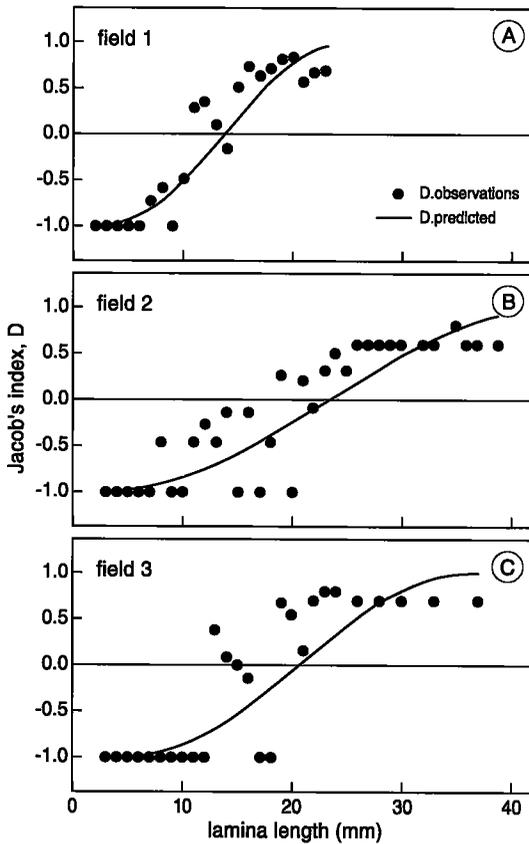
Fig. 3. Relationship between Jacob's preference Index transformed (*D'*) and *Phleum pratense* lamina length. *D'* ranges from -1 (complete avoidance) to +1 (exclusive preference). (A-C: field 1, field 2 and field 3). Data were cosine transformed and predicted curves are based on the back transformation of values from the following linear relationships: Field 1: $D' = 3.523 - 0.143*L$ (Lamina length), $n = 21$, $P < 0.0001$, $r^2 = 0.84$. Field 2: $D' = 3.338 - 0.076*L$, $n = 33$, $P < 0.0001$, $r^2 = 0.71$. Field 3: $D' = 3.618 - 0.099*L$, $n = 26$, $P < 0.0001$, $r^2 = 0.67$.

Fig. 4. Relationship between N-content and length classes of *Phleum pratense* lamina. Spearman Rank Correlation: $r_S = -0.5556$, $n = 53$, $P < 0.0001$. Bars indicate mean values ± SD.

Fig. 5. Profitability (N intake, mg per peck) and increasing length of *Phleum pratense* lamina. (based on biomass/lamina length-relationship (Fox *et al.* 1998) and N-content from Fig. 4 this study). Spearman Rank Correlation: $r_S = 0.9833$, $n = 9$, $P < 0.0001$.

smaller scale by removing the most profitable from a range of available a0 lamina sizes. Normally there is an interaction between length and quality of grass leaves (i.e. the longer the lamina, the lower the protein content (Holmes 1980; Fox 1993)). However, this was not the case in this study because there was little change in N-content
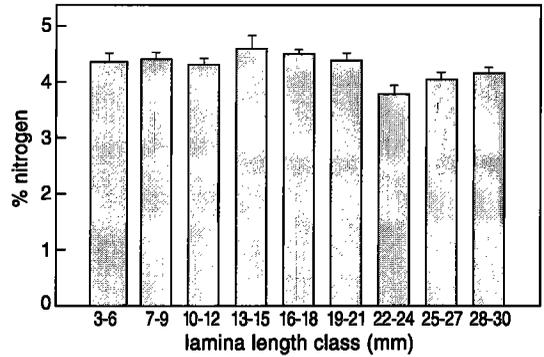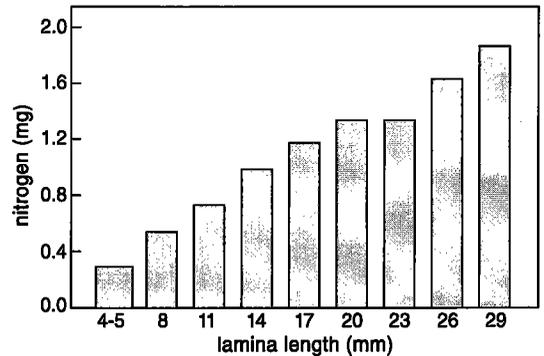
amongst the different available length classes. By selecting the larger laminae the geese obtained both the most N and biomass per bite from the range available (Fig. 5). This pattern occurred in all three study fields. However, feeding on the sward of lowest mean lamina length (i.e. the high lamina density field) had a cost relative to feeding in lower lamina densities.

There may be two reasons for the observed selection pattern: either the geese take the larger

laminae because they are aware of the higher quality of these and/or simply because they are more easily detected. It is likely that not all lamina sizes are detected with similar ease. Thus, larger laminae are probably more conspicuous than smaller ones. We cannot dismiss either of the two explanations, but either mechanism results in maximum intake rates amongst the geese. Despite the selectivity thresholds, some less profitable laminae were taken (i.e. in field 1) and the observed selection deviated slightly from perfect. The reason for this might be that the shoots in the different size classes were not evenly distributed. Hence, in an area of high density of short laminae it might still be profitable for the goose to take some less profitable laminae (rather than take none) before moving to another patch simply to maintain food intake rate.

Handling time has been shown to relate to bite size such that the larger the shoot the slower the peck rate (Owen 1972; Mayhew & Houston 1998). There may therefore be a cost to the geese to select for the larger laminae. It seems unlikely, however, given the relatively small differences between the preferred mean laminae of the different fields, that the geese in this study would show different peck rates. The range of lamina lengths taken during this study are generally much shorter than those, for instance, taken on the wintering grounds (e.g. Owen 1972; Therkildsen & Madsen 1999). We would expect geese to show adaptations which enable the time spent on staging areas to be put to best use, and we consider that the selection of longest laminae ensures highest biomass and maximum nitrogen per peck. This, together with the selection at the sward/plant/lamina level, maximises nutrient acquisition at this critical time of the year.

ACKNOWLEDGEMENTS

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SAMENVATTING

Foeragerende dieren zijn in de regel selectief en prefereren prooien c.q. planten met een relatief hoge energieopbrengst of met een hoog gehalte aan een bepaalde gewenste stof. Wanneer ze hun prooi niet in zijn geheel eten, prefereren ze de delen die de hoogste opbrengst hebben. Dit geldt ook voor grazende ganzen, die naar deze studie laat zien, zelfs nog een stap verder kunnen gaan in hun selectiviteit. Op IJsland werden in het voorjaar Kolganzen *Anser albifrons flavirostris* bestudeerd, die foerageerden op Timothee Gras *Phleum pratense* tijdens het opvetten voor de laatste etappe van hun trek van de Britse Eilanden naar Groenland. Eerder werk had al laten zien dat ze van dit gras vrijwel uitsluitend de meest profijtelijke type blaadjes eten, de zogenaamde a0 lamina. Al grazend weten de ganzen daarnaast ook nog de planten te selecteren met de grootste a0 lamina. Ook dit is profijtelijk, omdat de hoeveelheid eiwit toeneemt met de lengte van de lamina, zodat een afgebeten groot blaadje meer opbrengt dan een klein. Onduidelijk is of de ganzen deze relatief grote blaadjes actief opzoeken, of dat het hier een vorm van passieve selectie betreft: wellicht vallen grotere lamina beter op. In ieder geval eten de ganzen niet alleen het beste bladtype, maar ook de meest profijtelijke groottes. De ondergrens voor selectie is niet overal gelijk, maar varieert met het aanbod ter plaatse. In een veld waar alle planten relatief klein zijn, worden weliswaar de grootste lamina geselecteerd, maar deze kunnen zo klein zijn, dat ze elders, waar de planten groter zijn, geweigerd dan wel gemist worden. (MFL)