Feeding patch selection by herbivorous Anatidae: the influence of body size, and of plant quantity and quality

Daphné Durant, Hervé Fritz and Patrick Duncan

Recent findings suggest that herbivores select feeding sites of intermediate biomass in order to maximise their digestible nutrient intake as the result of the trade-off between forage quality and quantity ('forage maturation hypothesis'). We propose a reformulation of this hypothesis which recognises this trade-off, but also underlines that constraints due to body mass (i.e. metabolism and digestive constraints, size of the feeding apparatus) can lead to variations in grazing patterns. We tested this latter hypothesis experimentally in three species of herbivorous Anatidae of different body mass: the wigeon *Anas penelope* (in our study c. 620 g), the barnacle goose *Branta leucopsis* (c. 2000 g), and the greylag goose *Anser anser* (c. 3500 g). Each species was tested separately from 0600 to 0930 hours, in an enclosure with a mosaic of patches of grass of three different heights: short, medium and tall. The behaviour, and the location (i.e. patch) of each individual were recorded every 5 minutes. Our results show important interspecific differences in intake rates resulting in different feeding site selection: wigeon and barnacle goose fed fastest on the shortest swards, and selected short grass which was also of higher quality. Tall grass provided the highest dry matter intake rate and digestible protein intake for greylag geese, and they preferred these swards. These choices allowed the birds to maximise their digestible nitrogen intake rate rather than dry matter intake rate and our results thus underline the importance of nitrogen as a major currency for foraging decisions in herbivorous Anatidae. Since the birds selected the two extreme sward heights (instead of the medium one), the results give support to our hypothesis and underline the role of body size as an important cause of variations in patch selection in herbivorous Anatidae.

D. Durant (correspondence), H. Fritz and P. Duncan, CNRS, UPR 1934, Centre d'Etudes Biologiques de Chizé, 79360, Beauvoir-sur-Niort, FRANCE. Present address of D. Durant: Institut National de la Recherche Agronomique – Domaine du Bois Maché, 17450, Saint-Laurent-de-la-Prée, France. E-mail: durant@stlaurent.lusignan.inra.fr

Foraging theory postulates that decisions made by a foraging animal optimise acquisition of some currency (Stephens and Krebs 1986) which determines its fitness (Schoener 1971). This currency has often been assumed to be the net rate of dry matter intake, which has led to the formulation of the 'intake rate maximisation theory' (Krebs and McCleery 1984). Selection of feeding sites by vertebrate herbivores has been studied frequently, in particular in relation to patchy food resources (Langvatn and Hanley 1993, Weckerly 1994, Wilmshurst et al. 1995, Hupp and Robertson 1998). In support of the 'intake rate maximisation theory', it has been shown that sheep prefer grazing in patches offering the highest dry matter intake rates (Kenney and Black 1984, Illius et al. 1992), as do goats (Illius et al. 1999) and cattle (Demment et al. 1993).

However, as grasses mature, high biomass patches where the animals can achieve the highest dry matter intake rates, tend to be of poorer quality, i.e. to have higher fibre content, lower digestibility (Nehring and Nerge 1966, Prop and Vulink 1992), and lower nutrient contents (Summers and Critchley 1990). In addition, some studies have shown that phenolic compounds and other secondary metabolites accumulate as leaves grow

(Palo and Robbins 1991). Herbivores should therefore trade-off the intake rate of dry matter against that of nutrients in many contexts. This has been formulated as the 'forage maturation hypothesis', which states that herbivores should select for patches with intermediate plant biomass which allow the maximum net intake rate of digestible nutrients (Wilmshurst et al. 1995).

Grazing Anatidae are small vertebrate herbivores, and hence experience major constraints in the digestion of plants and require nutrient-rich food, which explains why they are selective grazers (Owen 1979, Gauthier and Bédard 1990, Conover 1991). Food choice in geese has been explained in terms of the nutrient contents of grasses, particularly nitrogen (Buchsbaum et al. 1981, 1986). Indeed, geese have a high nitrogen requirement as a result of their relative inefficiency in incorporating protein because the proteins in plants and avian tissues have different amino acid profiles (Sedinger 1984). In the trade-off between quality and quantity, birds will therefore be expected to favour quality to a greater extent than mammalian herbivores (Drent and Prins 1987, Stahl 2001).

The 'forage maturation hypothesis' has been tested in brent geese *Branta bernicla* on pastures (Riddington et al. 1997, Hassall et al. 2001) and the birds did trade-off quantity for quality, and nitrogen apparently played a key role. They selected grass of intermediate height for which the intake rate of nitrogen is higher. According to the concept of Riddington et al. (1997), this optimum results from a decelerating (type II) functional response (i.e. the relationship between the dry matter intake rate and plant biomass, Holling 1959), and the decreasing nitrogen content of grass with increasing sward height (see Bos et al. 2002 for a review). However, a variety of shapes of functional responses have been found in grazing Anatidae (Van der Wal 1998, Rowcliffe et al. 1999, Therkildsen and Madsen 2000, Hassall et al. 2001, Lang and Black 2001, Durant et al. 2003). For instance, Durant et al. (2003) found no significant variation in the instantaneous intake rate of the barnacle goose *Branta leucopsis* with increasing grass height, i.e. no functional response. In this case, with respect to food quality changes with grass height, one would expect barnacle geese to prefer grazing on short swards, instead of swards with medium height as predicted by the 'forage maturation hypothesis'. Moreover, in grazing vertebrates, the patterns of selectivity of feeding sites are likely to vary with differences in body mass because metabolic requirements and the ability to process and digest food are strongly correlated with body mass (Demment and Van Soest 1985), i.e. larger herbivores are less able to maintain intake rates on shorter swards but are capable of tolerating poorer quality plants (taller swards) than smaller herbivores (Illius and Gordon 1987, Wilmshurst et al. 2000, Durant et al. 2003). For these reasons, it seems unlikely that intermediate bio-

mass automatically allows for maximum intake of digestible nutrients. One would therefore expect more subtle differences in grazing patterns between species, because several ecological studies have already shown ecological separation of species or grazing successions according to (at least) body size (Illius and Gordon 1987, Prins and Olff 1998, Wilmshurst et al. 2000).

We thus suggest the hypothesis that the optimal grass biomass for a herbivore will depend on: (1) the differences in quality between patches of different biomass, (2) the shape of the functional response of the animal, and (3) the body size of the herbivore, which determines its nutrient requirements, the size of its feeding apparatus, as well as its digestive constraints.

In this study, we investigated how different relationships between intake rate and plant biomass, as well as differences in body mass, affect choices of patches of different quality. We used an experimental approach on controlled swards with three species of grazing Anatidae: the wigeon *Anas penelope* (mean body mass of individuals: 620 g), the barnacle goose (2000 g) and the greylag goose *Anser anser* (3500 g).

Material and methods

Experimental design

The experiments were conducted at the Centre d'Etudes Biologiques de Chizé, from 12–29 July 2000 in a 1 m high wire enclosure (7.5 × 9 m) where rye grass *Lolium perenne* seeds were planted with fertiliser in autumn 1999. Rye grass is naturally consumed by the three species (Owen 1973, Newton et al. 1974, Williams and Forbes 1980, Prop and Vulink 1992). The vegetation was divided into six 2.5 × 2.5 m replicate patches of three different treatments corresponding to three average grass heights: short, 2.0–3.0 cm and 58 ± 8 g dry weight/m² ($\pm$ S.D.); medium, 5.0–6.0 cm and 125 ± 15 g/m²; tall, 10.0–11.0 cm and 188 ± 36 g/m². The patches of the different treatments were placed so that each treatment occurred in each row (Fig. 1).

Vegetation characteristics

The day before each experimental series (see below), we measured vegetation height and biomass to ensure that these values were consistent across trials. Grass height was assessed in each patch by taking fifteen measures at random to the nearest 0.5 cm using a 'sward stick', a sliding square of polystyrene (area 16 cm², mass about 360 mg) on a graduated stick (Summers and Critchley 1990). This measure was done again at the end of a series in order to control for grass growth. As the vegetation grew rapidly in the short and medium treatments, the grass was cut between consecutive series. The biomass

Fig. 1. The enclosure with the 2.5 × 2.5 m patches of three treatments differing in their mean grass height; short: 2.0–3.0 cm, medium: 5.0–6.0 cm and tall: 10.0–11.0 cm.
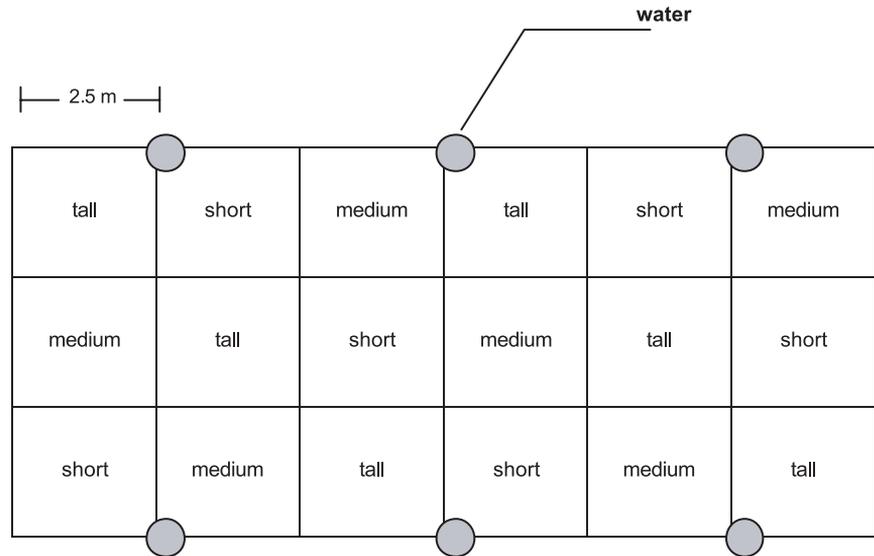
was measured by clipping the grass to the soil level within two 25 × 25 cm quadrats in two patches for each treatment. The grass was then oven-dried for 48 h at 60°C and weighed to the nearest 0.1 gram (dry weight, DW).

Apical parts of leaves (the plant part consumed in preference by grazing Anatidae, Therkildsen and Madsen 1999) were collected with a pair of scissors within each patch just before the beginning of the trials, dried and analysed for crude protein content (Kjeldahl nitrogen × 6.25) at Chizé, and for fibre content: ADF (acid detergent fibre) by the method of Van Soest (Van Soest 1982) in the laboratory of the *Institut National de la Recherche Agronomique* of Lusignan.

Intake rate measurements

To estimate the instantaneous intake rates of these species on the swards of different heights, we used data from another experimental study designed to assess the functional response of the birds. We summarize here the experiments, and detailed descriptions of them are given in Durant et al. (2003): we used captive birds, 10 European wigeon (5 males, 5 females), 10 greylag geese (2 males, 8 females) and 6 barnacle geese (4 males, 2 females), and each had a colour ring for individual identification. In the early morning or in the late afternoon, after a fasting period of 10–12 h, birds (a flock of a single species at a time) were allowed to graze in a 7.5 × 10 m enclosure of rye grass (at Chizé) maintained at the desired height (8 different treatments; from 1 to 12 cm), where fresh water was provided in two

bowls. The birds were allowed to graze freely, and the total time spent feeding by an individual (i.e. vigilance periods excluded) was recorded. The experiments were stopped after 25 minutes from the beginning of active foraging by the flocks, and birds were then put in individual boxes to collect all the droppings. These were then dried at 60°C for two days, weighed and ground through a 1 mm screen. Each bird was tested three times in the different height treatments, with at least one day between experiments.

We calculated the digestibility of organic matter (ash free dry weight = AFDW) using ADF as a marker (Summers and Grieve 1982, Prop and Deerenberg 1991, Manseau and Gauthier 1993) as:

$$\text{Digestibility (\% AFDW)} = [1 - (M_g/M_d)] \times 100$$

where M_g and M_d are ADF contents of grass and droppings, respectively (% AFDW). For each treatment we determined the mean digestibility for each bird by pooling approximately equal dry weights of droppings from each test (n = 3, range: 1–4). Analyses of ADF and ash contents of faeces were done on a single sub-sample per replicate.

Knowing the digestibility of AFDW for each bird, the quantity of grass ingested was calculated as :

$$\text{Intake (g AFDW)}$$
$$= \text{mass of faeces (g AFDW)}/(1 - \text{digestibility})$$

The dry weight (DW) of grass ingested was then calculated from the ash free measures using the measured ash content of the grass. Instantaneous intake rate (mg DW/min) was estimated by dividing amount of grass consumed (g DW) by the total grazing time. The

146

three replicates were averaged to give a single value of instantaneous intake rate per individual and per treatment.

Patch use trials

In the patch use trials, we used 6 of the 10 European wigeon (3 males and 3 females) in the functional response experiments, as well as 6 of the 10 greylag geese (2 males and 4 females) and the 6 barnacle geese (4 males and 2 females).

Two weeks before the beginning of the trials, the animals were habituated to the enclosure and the mosaic of patches. The trials were conducted on three consecutive days, one species tested per day, and repeated so that each species was tested three times (three series of three days) with 5–6 days between two consecutive series. The sequence of the species varied between series. The trials were run between 0600 and 0930 hours, after fasting the birds for one night. At the beginning of a trial, the six birds of a single species were allowed to enter the enclosure and to move freely among the patches. Fresh water was provided in 6 water sources as indicated in Fig. 1. Observations were made with binoculars from a car parked 10–15 m from the enclosure. The feeding patch and the behaviour (grazing/no grazing) of each individual was noted every 5 minutes (scan sampling, Altmann 1974). Immediately after the trial, the animals were moved into another enclosure where food (poultry pellets and grass) and water were available *ad libitum*.

Test of the hypothesis

The digestibility of crude protein in foliage is not affected by body mass in herbivorous Anatidae (Van Eerden 1998), and was assumed to be the same for the three species. It was also assumed to be the same for the three treatments: an increase in crude fibre content is known to lower the organic matter digestibility of the food in geese (Nehring and Nerge 1966, Prop and Vulink 1992), but the fibre content of the grass was nearly the same within the three treatments (see below). The digestibility of protein was thus estimated as 40 % for rye-grass (see Van Eerden 1998).

For the purpose of this study, we used the measures of instantaneous intake rate of dry matter (mg DW/min) from the functional response experiments for three sward classes: the short sward was 1–4 cm and 20–40 g/m^2; the medium, 5–9 cm and 70–110 g/m^2; and the tall, >11 cm and >150 g/m^2. The mean instantaneous intake rate of digestible protein (mg DW/min) was calculated for each treatment and for each species by multiplying the intake rate of dry matter by the protein content (proportion of DW) and by protein digestibility (0.40).

Data analysis

T-tests were performed to examine differences in protein and ADF contents between treatments, after arcsine transformation of proportions (Sokal and Rohlf 1995). Mean percentages quoted in the text are back transformed.

For each species, we tested for differences between sward heights in protein intake rate and dry matter intake rate using the residual maximum likelihood method (REML; Robinson 1987). Sward height was considered as a fixed effect and individuals and trial number as random effects. T-tests were then used to test for differences between pairs.

We tested for sward preferences among the three species of birds (SPECIES), individuals (IND), and trials (TRIAL), using the number of grazing observations for each sward height. We tested if the distribution of grazing events was random (Poisson distribution) using a generalised linear model with a log-link function (PROC GENMOD of SAS, SAS Institute Inc. 1999). We first fitted the triple interaction SPECIES × TRIAL × IND, then we tested whether the grass height (HEIGHT) had an effect on the distribution of the grazing birds on its own, and if it was similar among the three bird species (HEIGHT × SPECIES). Using the chi-squared statistic, we compared patch occupancy with the predicted occurrence of grazing events.

In order to test for differences in the number of grazing events between pairs of patches in different treatments, we used a REML, with HEIGHT as a fixed effect and IND and TRIAL as random effects.

Results

Vegetation parameters

Changes in grass heights during the study period were negligible, the height of the short treatment in the third series increased by 0.3 cm on average (Wilcoxon test: Z = 2.21, P = 0.03, n = 6 patches) and tended to decrease in tall grass in the three series, although not significantly (all P > 0.05). This is likely to have been due to trampling by birds, and not to grass depletion.

The short grass contained significantly more crude protein than the medium (t = 4.09, P = 0.004; Fig. 2a), and tall grass (t = 4.16, P = 0.003), between which no differences were found (t = 0.54, P = 0.61). The ADF contents were not different between the three treatments (S/M: 0.85, P = 0.42; M/T: t = −1.25, P = 0.25; S/T: t = −0.51, P = 0.62; Fig. 2b).
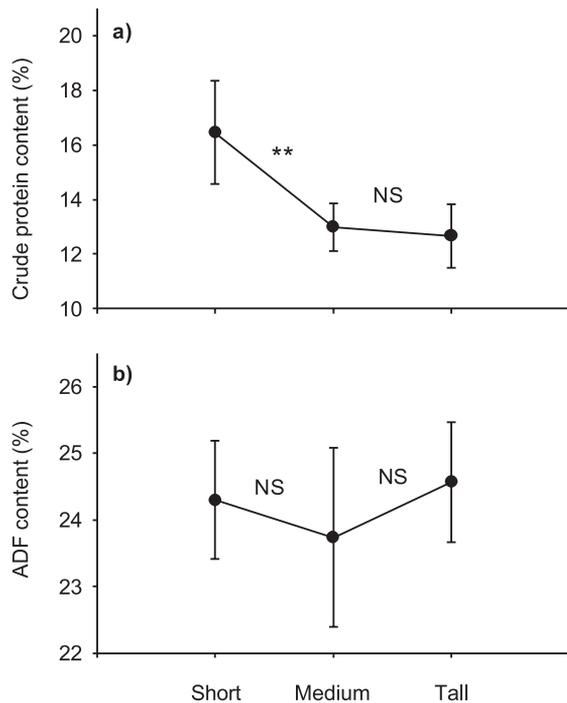
Fig. 2. Mean values ($\pm$ S.D.) of: a) crude protein content (%), and b) ADF content (%) of grass in the three treatments. Each dot is the mean of six values (one value per patch).

Patch preferences

The significant SPECIES $\times$ TRIAL $\times$ IND interaction indicates that there were variations among individuals which differed among trials and species (Table 1). Having controlled for this variation, the number of grazing events varied significantly with HEIGHT, but the three species did not respond to the different grass heights in the same manner (significant HEIGHT $\times$ SPECIES interaction, Table 1): wigeon and barnacle goose selected for short grass, and greylag goose for tall (Fig. 3a). This was confirmed by the REML, which showed that in wigeon and barnacle geese there were significantly more grazing observations in short than in medium ($F_{1,27} = 24.75$, P = 0.0001, and $F_{1,27} = 12.36$, P = 0.0016, respectively), and in medium than in tall grass ($F_{1,27} = 25.67$, P = 0.0001, and $F_{1,27} = 6.70$, P = 0.015, respectively). Conversely, greylag geese showed a preference for tall over short and medium ($F_{1,27} = 31.24$,
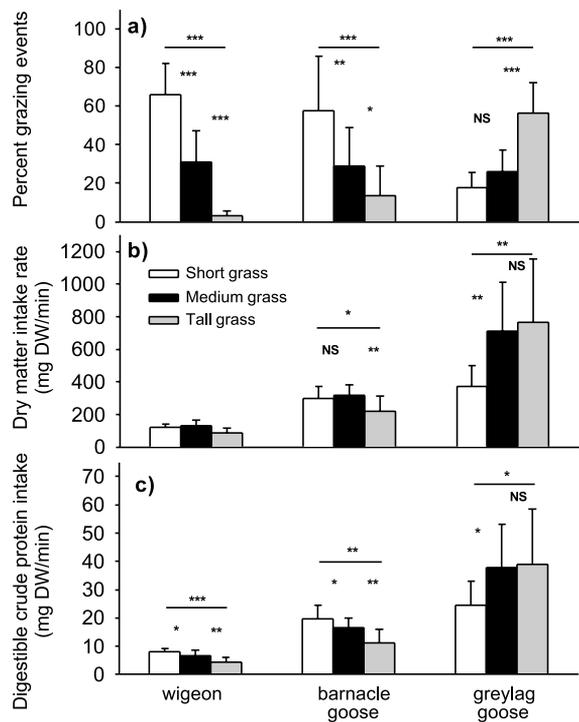

Fig. 3. Values of: a) percentage of grazing events ($\pm$ S.D.), b) dry matter intake rate ($\pm$S.D., mg DW/min), and c) digestible crude protein intake ($\pm$S.D., mg DW/min) for the three species during the three treatments. *: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$.

P = 0.0001, and $F_{1,27} = 29.79$, P = 0.0001, respectively), and no difference between short and medium grass ($F_{1,27} = 0.84$, P > 0.05).

Calculated intake rates

There was a significant overall height effect on the dry matter intake rate of barnacle and greylag geese (Fig. 3b; REML, $F_{2,33} = 4.60$, P = 0.02 and $F_{2,38} = 6.20$, P = 0.005, respectively), but not for wigeon ($F_{2,60} = 1.69$, P = 0.19). Dry matter intake decreased in the tallest grass for barnacle geese, whereas in greylag geese the lowest intake rate was found on the short grass.

When the intake rate of digestible crude protein was calculated, all species showed differences between treatments (Fig. 3c; wigeon: $F_{2,60} = 3.85$, P = 0.03; barnacle goose: $F_{2,33} = 8.05$, P = 0.001; greylag goose: $F_{2,38} = 3.06$, P = 0.05). The protein intake declined regularly

Table 1. Results of the fitted Poisson distribution based on a generalised linear model with a link function.

Source	Deviance	DF	χ^2	$P > \chi^2$
Intercept	539.40			
SPECIES $\times$ TRIAL $\times$ IND	441.76	53	97.64	0.0002
HEIGHT $\times$ SPECIES	196.45	4	179.11	< 0.0001
HEIGHT	375.56	2	66.20	< 0.0001

with increasing biomass for wigeon and barnacle geese, while in greylag geese only the low biomass treatment differed significantly from the two others, suggesting an asymptotic response, as in dry matter intake.

Discussion

These three species differ greatly in their intake rates (both dry matter intake rate and protein intake rate) during the different treatments. Wigeon and barnacle geese were similar in the shape of their relation between dry matter intake rate and sward characteristics, and maintained high intake rates on short swards. Conversely, for greylag geese, intake of dry matter was highest in the medium and tall swards. The pattern of differences in intake rates therefore corresponded with the pattern of patch selection in greylag geese, but not in the others.

The results for digestible protein intake rates fitted the pattern of patch selection in the two smaller species, though the selection for short grass was much stronger than the differences in digestible protein intakes. For greylag geese too, the birds selected their preferred treatment (the tall grass) more strongly than expected from differences in intake rates of digestible proteins.

Our results strongly support the idea that digestible crude protein intake is central in the foraging decisions of grazing Anatidae, as do those of Therkildsen and Madsen (1999), Vickery and Gill (1999), and Kristiansen et al. (2000) with field observations, and those of Riddington et al. (1997), Hassall et al. (2001) and Bos et al. (2002) with experiments. It was argued, for example, that brent geese maximise their rates of protein intake when they revisit previously grazed sites (Prins et al. 1980, Ydenberg and Prins 1981). The most likely explanation for this is related to the feeding strategy of these birds. Since they have high daily energy requirements but a simple gut and a limited ability to digest fibre (Marriott and Forbes 1970, Sedinger et al. 1989), they rely more on ingesting large quantities of grass with the highest content of soluble nutrients (Ydenberg and Prins 1981).

In the present study, we used the measurement of nitrogen as an index of available protein, but we are conscious of the fact that it is not the best measure of protein in plant material, especially since herbivorous Anatidae are very efficient in extracting a high proportion of soluble protein, but are much less able to obtain other proteinaceous material locked up in cell walls. If this latter fraction increases with leaf growth as a proportion of the crude protein measured by nitrogen determination, we over-estimated the protein intake rate, especially in the taller swards. We assumed protein digestibility to be 40% for the three treatments (Van Eerden 1998), and it was not possible to check this assumption by measuring digestibility of protein directly

from droppings since these were not issued from homogeneous swards (i.e. 'partial preferences', the birds explored and grazed the three types of patches). Moreover, this experiment did not really allow a clear test of our hypothesis, since nitrogen content showed no significant difference between medium and tall grass, and ADF content did not vary with grass height. This implies that the major factors contributing to the bird selectivity were represented only in a two-phase state (i.e. high protein content:short swards, and lower protein content:medium and tall swards).

The three grazing Anatidae tested here did not select for intermediate sward heights (or biomass), in contrast to the brent goose studied by Riddington et al. (1997) and Hassall et al. (2001). The birds selected the two extreme treatments: low biomass for wigeon and barnacle goose, and high biomass for greylag goose. These choices allowed them to maximise their protein intake rate. This shows that the result of a trade-off between grass quantity and quality can lead to different grazing patterns. The differences can be related to differences in body size (i.e. energetic requirements), in the shape of the functional responses and/or in the actual relationship between biomass and quality in the different swards. Wigeon and barnacle goose were more efficient on the shortest swards, which in our experiments, and in natural environments, have the highest protein contents (Fig. 2; Summers and Critchley 1990). The differences in protein intake rate between the short and medium swards were in fact due to differences in protein content, as dry matter intake rate did not differ between these swards for either species. Consequently, there was no trade off to be made between quantity and quality, although this may occur if dry matter intake rate drops strongly on very short swards. For greylag geese, the difference in dry matter intake rate between treatments was such that even with differences in protein content between swards, high grass biomass provided a high protein intake rate. Greylag geese are prepared to sacrifice food quality and thus to forage on taller grass, if the intake rate on tall swards is sufficiently high. An explanation for the preference of greylag geese for tall swards against medium ones, even in the absence of difference in digestible crude protein intake rates between these two heights, could be that it may be easier for the geese to take long leaves than medium ones.

Our results show that the pattern of patch selection for a herbivorous Anatidae thus depends on differences between species in the shape of their functional responses, which may ultimately reflect differences in body mass and the size of their bill (Durant et al. 2003). The greylag goose has the largest bill of the three species (see Durant et al. 2003 for measurements of bill size of the three species), which makes it difficult for them to harvest short swards. Moreover, they have a limited ability to compensate for small peck sizes by increasing

peck rates on short swards, and thus they achieve high intake rates on medium and tall swards only. In contrast, smaller species, such as the barnacle goose and the wigeon, are able to handle and process short and nutritious swards more easily with their smaller bills, and have a greater capacity to increase pecking rates when peck sizes are low. Their intake rates are quite constant. Only handling time (in particular time to crop swards) becomes a constraint on intake rate at high plant biomass. As in ungulates, the functional response is thus the result of the animals' ability to process swards, which depends greatly on the size and the morphology of their bill/mouth (Shipley and Spalinger 1992).

Finally, body mass seems to be an important determinant of interspecific differences in foraging site selection of herbivorous Anatidae ('allometry of food selection'). The two smallest species, wigeon and barnacle goose, have higher mass-specific metabolic demands than the larger greylag goose (mass-specific Daily Energy Expenditure DEE in wigeon: 8.34 $W/kg^{0.75}$, in barnacle goose: 7.30 $W/kg^{0.75}$ and in greylag goose: 6.48 $W/kg^{0.75}$, according to Van Eerden, 1998; see also Peters 1983), and are likely to be more constrained by nutrient intake, especially nitrogen. In the same way, greylag geese being larger than wigeon and barnacle geese, are much more restricted in their intake rate than wigeon and barnacle geese on short swards (Durant et al. 2003), and thus should be less able to meet their energy requirements. This may explain why small species (wigeon and barnacle goose) prefer grazing on short swards, whereas larger ones (greylag goose) graze on taller grass (see Vickery and Gill 1999 for a review). Our results suggest that there is a separation of species according to their body mass for the grass height/biomass on which they optimise their main foraging currency, as it has been demonstrated in ruminants in the Serengeti ecosystem (Wilmshurst et al. 2000).

These results support the argument that body size and energy requirements have strong effects on sward selection. However, our results are likely to be state-specific since they were obtained in July, and using captive birds, starved overnight and foraging on artificial grass swards. It is possible that at other times of year and under other circumstances, foraging choices by birds could be different, reflecting changes in nutritional demand, for example. These possible variations set limits to the generality of this experiment in terms of the actual choices in sward heights, but not in terms of the influence of body mass and specific nutrient requirements.

Since intake rate is related to grass height in herbivorous Anatidae (Durant et al. 2003) and plant nutritive quality is too (Summers and Critchley 1990, Riddington et al. 1997), grass height is likely to be the cue used by birds to select feeding sites, as has been suggested in sheep (Illius et al. 1992). The extreme need for high quality food in these small herbivores seems to have led to strong selection for feeding efficiency on sparse, but rich food items. Comparisons between ungulate and herbivorous Anatidae foraging have a great potential to reveal general mechanisms in herbivore-plant interactions (Drent and Prins 1987). Understanding these processes also has important implications for the understanding of the habitat selection of the birds (Van de Koppel et al. 1996, Rowcliffe et al. 1998, Bos et al. 2002), as well as for improving pasture management in the context of species conservation (Vickery and Gill 1999).

References

Altmann, J. 1974. Observational study of behavior: sampling methods. – Behaviour 49: 227–267.
Bos, D., Drent, R., Rubinigg, M. and Stahl, J. 2002. The relative importance of food biomass and quality for patch and habitat choice in brent geese. – Ph.D. thesis, University of Groningen, The Netherlands.
Buchsbaum, R., Valiela, I. and Teal, J. M. 1981. Grazing by Canada geese and related aspects of the chemistry of salt marsh grasses. – Colon Waterbirds 4: 126–131.
Buchsbaum, R., Wilson, J. and Valiela, I. 1986. Digestibility of plant constituents by Canada geese and Atlantic brant. – Ecology 67: 386–393.
Conover, M. R. 1991. Herbivory by Canada geese: diet selection and effect on lawns. – Ecol. Appl. 1: 231–236.
Demment, M. W. and Van Soest, P. J. 1985. A nutritional explanation for body size patterns of ruminant and non ruminant herbivores. – Am. Nat. 125: 641–672.
Demment, M. W., Distel, R. A., Griggs, T. C., Laca, E. A. and Deo, G. P. 1993. Selective behaviour of cattle grazing ryegrass swards with horizontal heterogeneity in patch height and bulk density. – In: Proceedings of the XVII International Grassland Congress (New Zealand), New Zealand Grassland Association, Palmerston North, New Zealand. pp. 712–714
Drent, R. H. and Prins, H. H. T. 1987. The herbivore as prisoner of its food supply. – In: Van Andel, J., Bakker, J. and Snaydon, R. W. (eds). Disturbance in grasslands; species and population responses. Dr W. Junk Publishing Company, Dordrecht, pp. 133–149.
Durant, D., Fritz, H., Blais, S. and Duncan, P. 2003. The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size. – J. Anim. Ecol. 72: 220–231.
Gauthier, G. and Bédard, J. 1990. The role of phenolic compounds and nutrients in determining food preferences in greater snow geese. – Oecologia 84: 553–558.
Hassall, M., Riddington, R. and Helden, A. 2001. Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands:

effects of sward length and nitrogen content. – Oecologia 127: 97–104.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. – Can. Entomol. 41: 385–398.

Hupp, J. W. and Robertson, D. G. 1998. Forage site selection by lesser snow geese during autumn staging on the arctic national wildlife refuge, Alaska. – Wildl. Monogr. 138: 1–40.

Illius, A. W. and Gordon, I. J. 1987. The allometry of food intake in grazing ruminants. – J. Anim. Ecol. 56: 989–999.

Illius, A. W., Clark, D. A. and Hodgson, J. 1992. Discrimination and patch choice by sheep grazing grass-clover swards. – J. Anim. Ecol. 61: 183–194.

Illius, A. W., Gordon, I. J., Elston, D. A. and Milne, J. D. 1999. Diet selection in goats: a test of intake-rate maximization. – Ecology 80: 1008–1018.

Kenney, P. A. and Black, J. L. 1984. Factors affecting diet selection by sheep. I. Potential intake rate and acceptability of feed. – Aust. J. Agric. Res. 35: 551–563.

Krebs, J. R. and McCleery, R. H. 1984. Optimization in behavioural ecology. – In: Krebs, J. R. and Davies, N. B. (eds). Behavioural Ecology – an evolutionary approach. Blackwell Scientific Publications, Oxford, pp. 91–121.

Kristiansen, J. N., Fox, A. D. and Nachman, G. 2000. Does size matter? Maximising nutrient and biomass intake by shoot size selection amongst herbivorous geese. – Ardea 88: 119–125.

Lang, A. and Black, J. M. 2001. Foraging efficiency in barnacle geese Branta leucopsis: a functional response to sward height and an analysis of sources of individual variation. – Wildfowl 52: 7–20.

Langvatn, R. and Hanley, T. A. 1993. Feeding-patch choice by red deer in relation to foraging efficiency: an experiment. – Oecologia 95: 164–170.

Manseau, M. and Gauthier, G. 1993. Interactions between greater snow geese and their rearing habitat. – Ecology 74: 2045–2055.

Marriott, R. W. and Forbes, D. K. 1970. The digestion of lucerne chaff by Cape Barren geese Cereopsis novaehollandiae Latham. – Aust. J. Zool. 18: 257–263.

Nehring, K. and Nerge, I. 1966. Die Verdaulichkeit verschiedener Futterstoffe bei Gänsen. – Arch. f. Geflügelz. Kleintierk 15: 3–21.

Newton, I., Campbell, C. R. G. and Allison, A. 1974. Gut analyses of greylag and pinkfooted geese. – Bird Study 21: 255–262.

Owen, M. 1973. Cutting and fertilizing grassland for winter goose management. – J. Wildl. Manage. 39: 163–167.

Owen, M. 1979. Food selection in geese. – Verh. Orn. Ges. Bayern 23: 169–176.

Palo, R. T. and Robbins, C. T. 1991. Plant defenses against mammalian herbivory. – CRC Press, Inc.

Peters, R. H. 1983. Metabolism. – In: Beck, E., Birks, H. J. B. and Connor, E. F. (eds). The ecological implications of body size. Cambridge University Press, pp. 24–44.

Prins, H. H. T., Ydenberg, R. C. and Drent, R. H. 1980. The interaction of brent geese Branta bernicla and sea plantain Plantago maritima during spring staging: field observations and experiments. – Acta Bot. Neerl. 29: 585–596.

Prins, H. H. T. and Olff, H. 1998. Species-richness of African grazer assemblages: towards a functional explanation. – In: Newberry, D. M., Brown, N. and Prins, H. H. T. (eds). Dynamics of Tropical Communities. Blackwell Science, Oxford, pp. 449–490.

Prop, J. and Deerenberg, C. 1991. Spring staging in brent geese Branta bernicla: feeding constraints and the impact of diet on the accumulation of body reserves. – Oecologia 87: 19–28.

Prop, J. and Vulink, T. 1992. Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. – Funct. Ecol. 6: 180–189.

Riddington, R., Hassall, M. and Lane, S. 1997. The selection of grass swards by brent geese Branta b. bernicla: interactions between food quality and quantity. – Biol. Cons. 81: 153–160.

Robinson, D. L. 1987. Estimation and use of variance components. – Statistician 36: 3–14.

Rowcliffe, J. M., Sutherland, W. J. and Watkinson, A. R. 1999. The functional and aggregative response of a herbivore: underlying mechanisms and the spatial implications for plant depletion. – J. Anim. Ecol. 68: 853–868.

Rowcliffe, J. M., Watkinson, A. R. and Sutherland, W. J. 1998. Aggregative responses of brent geese on salt marsh and their impact on plant community dynamics. – Oecologia 114: 417–426.

SAS Institute 1999. SAS/STAT. – SAS Institute Inc., Cary, USA.

Schoener, T. W. 1971. Theory of feeding strategies. – Annu. Rev. Ecol. Syst. 2: 369–404.

Sedinger, J. S. 1984. Protein and amino acid composition of tundra vegetation in relation to nutritional requirements of geese. – J. Wildl. Manage. 48: 1128–1136.

Sedinger, J. S., White, R. G., Mann, F. E., Burris, F. A. and Kedrowski, R. A. 1989. Apparent metabolizability of alfalfa components by yearling Pacific black brent. – J. Wildl. Manage. 53: 726–734.

Shipley, L. A. and Spalinger, D. E. 1992. Mechanisms of browsing in dense food patches: effects of plant and animal morphology on intake rate. – Can. J. Zool. 70: 1743–1752.

Sokal, R. R. and Rohlf, F. J. 1995. Biometry, Third Ed. – W.H. Freeman and Co., New York.

Stahl, J. 2001. Limits to the co-occurence of avian herbivores– How geese share scarce resources. – Ph.D. thesis, University of Groningen, The Netherlands.

Stephen, D. W. and Krebs, J. R. 1986. Foraging theory. – Princeton University Press.

Summers, R. W. and Critchley, C. N. R. 1990. Use of grassland and field selection by brent geese Branta bernicla. – J. Appl. Ecol. 27: 834–846.

Summers, R. W. and Grieve, A. 1982. Diet, feeding behaviour and food intake of the upland goose (Chloëphaga picta) and ruddy-headed goose (C. Rubidiceps) in the Falkland islands. – J. Appl. Ecol. 19: 783–804.

Therkildsen, O. R. and Madsen, J. 1999. Goose grazing selectivity along a depletion gradient. – Ecography 22: 516–520.

Therkildsen, O. R. and Madsen, J. 2000. Assessment of food intake rates in pink-footed geese Anser brachyrhynchus based on examination of oesophagus contents. – Wildl. Biol. 6: 167–172.

Van de Koppel, J., Huisman, J., Van der Wal, R. and Olff, H. 1996. Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. – Ecology 77: 736–745.

Van der Wal, R., 1998. Defending the marsh – Herbivores in a dynamic coastal ecosystem. – Ph.D. thesis, University of Groningen, The Netherlands.

Van Eerden, M. 1998. Patchwork: Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands. – Ph.D. thesis, University of Groningen, The Netherlands.

Van Soest, P. J. 1982. Nutritional Ecology of the Ruminant: Ruminant metabolism, Nutritional Strategies, the Cellulotic Fermentation and the Chemistry of Forages and Plant Fibres. – O & B Books, Corvallis.

Vickery, J. A and Gill, J. A. 1999. Managing grassland for wild geese in Britain: a review. – Biol. Cons. 89: 93–106.

Weckerly, F. W. 1994. Selective feeding by black-tailed deer: forage quality or abundance? – J. Mammal. 75: 905–913.

Williams, G. and Forbes, J. E. 1980. The habitat and dietary preferences of dark-bellied brent geese and wigeon in relation to agricultural management. – Wildfowl 31: 151–157.

Wilmshurst, J. F., Fryxell, J. M. and Bergman, C. M. 2000. The allometry of patch selection in ruminants. – Proc. R. Soc. Lond. 267: 345–349.

Wilmshurst, J. F., Fryxell, J. M. and Hudson, R. J. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). – Behav. Ecol. 6: 209–217.

Ydenberg, R. C. and Prins, H. H. T. 1981. Spring grazing and the manipulation of food quality by barnacle geese. – J. Appl. Ecol. 18: 443–453.