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Using food quality and retention time to predict digestion efficiency in geese

Jouke Prop, Wouter D. Van Marken Lichtenbelt, Jan H. Beekman & Jan F. Faber

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Investigations of food digestibility are important in nutritional studies of herbivores, but accurate assessments in the field are usually difficult and time consuming. This study explored the possibility of predicting digestibility and metabolisability of organic matter from the chemical composition and retention time of food in barnacle geese *Branta leucopsis*. Captive birds were used in indoor trials to allow accurate assessments of digestion in terms of energy, organic matter and nutritional components. Retention times were estimated from dropping rates which were recorded by an electronic device. The regression models that best explained the variation in apparent digestibility and metabolisability of organic matter incorporated the proportion of cell walls in the food (acid detergent fibre had a negative effect) and the retention time (longer retention had a positive effect). To test the predictive power of the regression model, we performed seven field trials with captive barnacle geese on *Festuca rubra* salt marshes. The regression model proved reliable except when salt concentrations in the food were high following inundation by spring tides. The results obtained from this study further demonstrated its value in estimating the individual digestibility of each plant species in mixed diets. This is illustrated with reference to a study of food selection by brent geese *Branta bernicla*.

Key words: barnacle goose, Branta leucopsis, food retention, herbivores, metabolisability, nutrition

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Investigations of food digestibility form an important element in studies of energy balance in animals (Robbins 1993). However, estimating the digestibilities of food ingested by free-ranging animals is often difficult and time consuming. Natural markers in the food have been employed successfully to estimate food digestibilities in herbivores (Ebbinge et al. 1975, Karasov 1990), but this technique is laborious, requiring large efforts in collecting representative samples of food and faeces and in the subsequent chemical analyses of both (Lane &

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Hassall 1996). *In vitro* simulations of digestive processes were developed to overcome these problems (Goering & Van Soest 1970), but this technique is beset by analytical difficulties, and its validity for non-ruminants is uncertain (Schwartz & Hobbs 1985). A simpler approach is to predict digestibilities on the basis of the chemical composition of the food (Van Soest 1982). Such predictive regressions are extremely useful, both because they indicate the nutritive value of the food and because they explain why some plant species are better digested than others.

In this study, we explored predictive regressions in the barnacle goose *Branta leucopsis*. Geese are interesting study objects for this purpose because they have relatively simple digestive systems resulting in short retention time and a poor digestion of the food. Relative to the nutritional ecology of ruminants, that of hindgut fermenters such as geese has been little studied (Sedinger 1997), and the number of digestion trials linked to the ecology of birds in the wild is particularly low (Boudewijn 1984, Buchsbaum et al. 1986, Sedinger et al. 1989, Hupp et al. 1996). We aimed to apply the precision of indoor trials to direct observations of the foraging ecology of geese in the wild. Our study included (i) indoor digestion trials during which captive birds were provided with plants that were among their wild conspecifics' most important food species during winter and spring, and (ii) trials with captive geese on salt marshes.

The amount of energy that herbivores derive from their food depends on its chemical composition and on the digestive physiology of the animals (McWilliams & Karasov 1998). We therefore considered the effects both of the chemical composition of the food and of the length of time the food remained in the digestive system (the retention time). First, we identified the main correlates of digestion with features of the food and with the retention time. We further assessed the digestibility of the food in terms of its separate components (protein, fat and carbohydrates). Variation in retention time was achieved by offering food for different lengths of time per day in combination with exposing the geese to different light-dark regimes. Variation in food quality was achieved by providing food plants that were collected on different dates and from different habitats. The accuracy of the predictions of digestibility of organic matter that we inferred from linear regressions was subsequently tested against actual digestibilities obtained from feeding trials on natural vegetation. We further provide an example of food choice by wild brent geese *Branta bernicla* that indicates when the regression method is particularly useful.

Methods

Indoor digestion trials

Digestion trials were carried out with two barnacle geese that had been captured in February, two months before the onset of the trials. To avoid unwanted effects of artificial food on the digestive system (Owen 1975, Sibly 1981), the birds were kept on grass lawns. During the trials, the geese were housed in separate cages (of 1 × 1 × 1 m) in a room in which the temperature was maintained at 20 ± 2°C. The birds could see each other, which was a prerequisite for them to behave quietly. Two types of food were available *ad libitum*: (i) *Festuca rubra*, collected from coastal marshes on three dates in the spring, and (ii) a mixture of *Lolium perenne* and *Poa* spp., collected from inland pastures. The mower chopped the grass in pieces of 1-4 cm, which is approximately the size of leaves that wild geese ingest (Prop et al. 1998, Kristiansen et al. 2000). Both types were stored at -20°C. *Festuca* was provided for 12 light hours per day (09:00-21:00) while the *Poa/Lolium* mix was provided for 12, 16 and 23 light hours per day to enable the geese to retain the food for longer periods. Each test was composed of a two-day conditioning period to allow the birds to habituate to the experimental situation followed by a three-day digestion trial. Droppings passed through the wire-mesh floors of the cages and were collected on plastic trays. Each dropping was registered by a sensor attached to the tray, and the times of production were stored in a data logger. For each trial an average interval between successive droppings was calculated. Droppings were removed every six hours during the light periods and immediately weighed to determine their fresh mass. The batch collected after the subsequent hours of darkness (at 08:00) was allocated to the dropping production of the previous day. The droppings from each day were homogenised and two subsamples of 300 g each were freeze dried to determine the water content for conversion of fresh dropping mass into dry weights. To prevent spilled food mixing with the droppings, the grass was presented in dispensers mounted against the cages; these were replenished every six hours. The amount of food consumed was determined as the total mass provided minus food remaining or spilled. Subsamples of 500 g were freeze dried to determine the water content and were stored for later chemical analyses. The geese were weighed regularly from the time of their capture and before and after each digestion trial. They maintained their average body mass of 1.68 kg (the daily weight change relative to initial body mass was on average -0.1 and -0.6% on *Poa/Lolium* and *Festuca*, respectively), but they did not show the increase in mass

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typical for wild individuals in the spring (Ebbinge et al. 1991).

Field trials

To validate the predictions of digestibility of organic matter derived from the indoor trials, we performed further digestion trials in the field. Two different barnacle geese were individually housed in large pens (100 m^2) located on *Festuca* swards on a salt marsh used by wild barnacle geese. The captive birds showed the same diurnal activity pattern as the wild ones. At night they were kept in a resting enclosure where they had no access to food. We carried out seven one-day experiments during March-April. The pens were placed on swards that had not been grazed for about one week, thus simulating the grazing regime of the wild geese (Ydenberg & Prins 1981). Immediately prior to the experiments, samples of *Festuca* were collected for later chemical analyses. On the trial days, all droppings were recovered for subsequent drying, weighing and analyses. Dropping intervals were calculated as the time during which the geese were active (which was similar to that during which they had access to food as they had only brief spells of resting) divided by the number of droppings produced.

Chemical analyses

Both food and droppings were ground through a 1-mm sieve and then analysed for total nitrogen (Kjeldahl), cell wall components (neutral detergent fibre (NDF) and acid detergent fibre (ADF); Goering & Van Soest 1970) and ash. Hemicellulose was calculated as the difference between the concentrations of NDF and ADF. In addition, samples from the indoor trials were analysed for crude fat (ether extract) and caloric content (by adiabatic bomb calorimetry). The fat content of *Festuca* in the field trials was estimated from the average values for the *Festuca* samples from the indoor trials. To distinguish between nitrogen from faeces (undigested proteins) and nitrogen from urinary waste products (mainly uric acid; Robbins 1993), we determined the nitrogen associated with proteins following the precipitation method of Terpstra & De Hart (1974). Crude protein (hereafter protein) in the food was calculated as the percentage of total nitrogen multiplied by 6.25 (Robbins 1993). Similarly, protein concentrations in the droppings were calculated from the nitrogen associated with proteins. The concentration of urinary products in the droppings was calculated from the percentage of uric nitrogen multiplied by three, given that urinary products contain 33% nitrogen (Terpstra & De Hart 1974). Soluble carbohydrates were estimated as the complement of ash, NDF, protein and fat. For the droppings, this amount was reduced by the concentration of urinary products. All concentrations were expressed on an organic matter basis (om, or ash-free).

Calculations and statistics

The apparent digestibility of component C (%) was calculated as:

$$D_c = \frac{F_c - (O_c \times R)}{F_c} \times 100 ,$$

where F_c = the proportion of component C in the ash-free dry mass of the food, and O_c = the proportion of C in the ash-free dry mass of the droppings. Component C stands for protein, soluble carbohydrates, fat, ADF and hemicellulose; R = the ratio of the ash-free dry mass of droppings to that of the food in the indoor trials, and the ratio of the ADF content of the food to that of the droppings in samples from the field trials. ADF is a reliable marker substance in spring (Prop & Vulink 1992) when the field trials were conducted. Calculating digestibilities would give the same results when concentrations and the mass of food and droppings were all expressed on a dry matter basis. The apparent digestibility of organic matter D_{om} was adjusted to account for possible nitrogen retention. If geese were in positive nitrogen balance, a corresponding amount of uric acid was added to the output of droppings (Miller & Reinecke 1984). A negative nitrogen balance was similarly adjusted. Because of the 33% nitrogen in uric acids (see above), the amount of uric acid was calculated by multiplying the amount of nitrogen retained by a factor 3:

$$D_{om} = \frac{F_{om} - (O_{om} \times R + (F_N - O_N \times R) \times 3)}{F_{om}} \times 100 ,$$

where F_N and O_N are the concentrations of nitrogen in food and droppings.

Likewise, the apparent metabolisability of the food (AM, %) was calculated as:

$$AM = \frac{F_{energy} - (O_{energy} \times R + (F_N - O_N \times R) \times 34.4)}{F_{energy}} \times 100 ,$$

where F_{energy} and O_{energy} are the energy content of the food and droppings (kJ. g^{-1} om), respectively. To convert the amount of nitrogen retained into energy values, we used a multiplication factor that represented the amount of energy required to excrete nitrogen (34.4kJ. g^{-1}; Miller & Reinecke 1984). The metabolisable energy of the food was calculated as the product of its apparent meta-

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bolisability and the energy content: ME = (AM / 100) × F_{energy}, kJ. g^{-1} om. The contribution of component C to the metabolisable energy was calculated as:

$$ME_c = (F_c \times D_c \times E_c) \times 10^{-4},$$

where C stands for protein, soluble carbohydrates, fat, ADF and hemicellulose, and E_c for the physiological energy content of component C. The energy contents of protein (17.8 $kJ.g^{-1}$, which accounts for the loss of part of the energy in urinary products), carbohydrates (17.6 $kJ.g^{-1}$) and fat (39.3 $kJ.g^{-1}$) were derived from Schmidt-Nielsen (1975).

Standard statistical tests were used to analyse the data (SPSS 1999). To analyse the relationships between digestibility and both the chemical composition of the food and the dropping intervals (i.e. the retention time), regression analysis was performed with a backward elimination procedure. Plant species and test bird were entered as dummy variables. To allow for the number of replicates for each trial, the variables representing the test birds were kept in all regressions. The results of each test of the field trials were averaged across the two test birds. Unless otherwise stated, average values are given as means ± SD.

Results

Indoor trials

The plant components that were best digested were proteins, followed by soluble carbohydrates, fat and NDF (Table 1). Protein and soluble carbohydrates together contributed most (75%) to the metabolisable energy. ADF and hemicellulose, which together were the largest components in the plants, provided only 16% of the metabolisable energy; for fats it was 9%.

The digestibility of organic matter was higher in *Poa/Lolium* than in *Festuca* (36.7 and 31.0%, respectively; $F_{1,9} = 33.40$, $P < 0.0005$). Similarly, the metabolisable energy was higher in *Poa/Lolium* than in *Festuca* ($F_{1,9} = 34.94$, $P < 0.0005$). In both, the metabolisability of energy was slightly higher than the digestibility of organic matter. The geese were in positive nitrogen balance during each of the tests and retained 0.33 (*Poa/Lolium*) and 0.88 (*Festuca*) g nitrogen per day.

Dropping intervals were shortest when the geese were feeding on *Festuca* (3.82 ± 0.83 minutes against 4.44 ± 0.72 minutes for *Poa/Lolium*; $F_{1,9} = 4.9$, $P = 0.05$) and the droppings were heavier (*Festuca*: 0.66 ± 0.19 g and *Poa/Lolium*: 0.36 ± 0.06 g; $F_{1,9} = 24.8$, $P = 0.001$). The dropping intervals were positively related to the concentration of protein in the food ($F_{1,8} = 9.2$, $P < 0.05$) and to the day length available ($F_{1,8} = 15.1$, $P = 0.005$).

We tested two methods for predicting the apparent digestibility of organic matter. First, because the digestibilities of the nutritional components differed (see Table 1), we expected that the apparent digestibility of the organic matter would vary with the chemical profile of the food. To obtain an estimate of the apparent digestibility of the organic matter, we therefore calculated the products of the concentration and the average digestibility of each of the nutritional components (see Table 1) and summed them as

$$D_{om} = \Sigma F_c \times D_c .$$

This method, however, proved adequate only in showing the large differences in apparent digestibility of organic matter between plant species ($F_{1,9} = 213.5$, $P <$

Table 1. Composition of food plants (in % of organic matter, om), the apparent digestibility of plant components (in %) and their contributions to apparent metabolisable energy (ME; in kJ/g om). Metabolisable energy was also derived from direct calorimetric measurements of food and droppings (rows marked as 'Energy'). Mean values ± SD for *Festuca rubra* (N = 6) and a mixture of *Poa* spp. and *Lolium perenne* (N = 6)

	Concentration	Apparent digestibility	ME
Festuca			
Protein	21.2 ± 3.4	72.2 ± 1.9	2.73 ± 0.51
Soluble carbohydrates	24.7 ± 2.2	57.2 ± 4.8	2.49 ± 0.39
Fat	6.7 ± 0.6	22.4 ± 2.1	0.59 ± 0.07
ADF	22.6 ± 0.6	-0.4 ± 2.2	-0.01 ± 0.08
Hemicellulose	24.8 ± 0.9	25.4 ± 6.0	1.10 ± 0.23
Organic matter (om)	100.0	31.0 ± 1.2	
Energy; kJ/g om	20.8 ± 0.1	32.1 ± 1.3	6.73 ± 0.18
Poa/lolium			
Protein	20.3 ± 0.5	71.6 ± 2.6	2.56 ± 0.13
Soluble carbohydrates	33.4 ± 1.2	59.3 ± 5.4	3.47 ± 0.33
Fat	6.6 ± 0.4	30.3 ± 6.3	0.79 ± 0.17
ADF	20.7 ± 0.6	3.1 ± 3.1	0.11 ± 0.11
Hemicellulose	19.0 ± 0.3	35.2 ± 6.5	1.18 ± 0.20
Organic matter	100.0	36.7 ± 2.8	
Energy	20.6 ± 0.03	39.3 ± 2.5	8.14 ± 0.53

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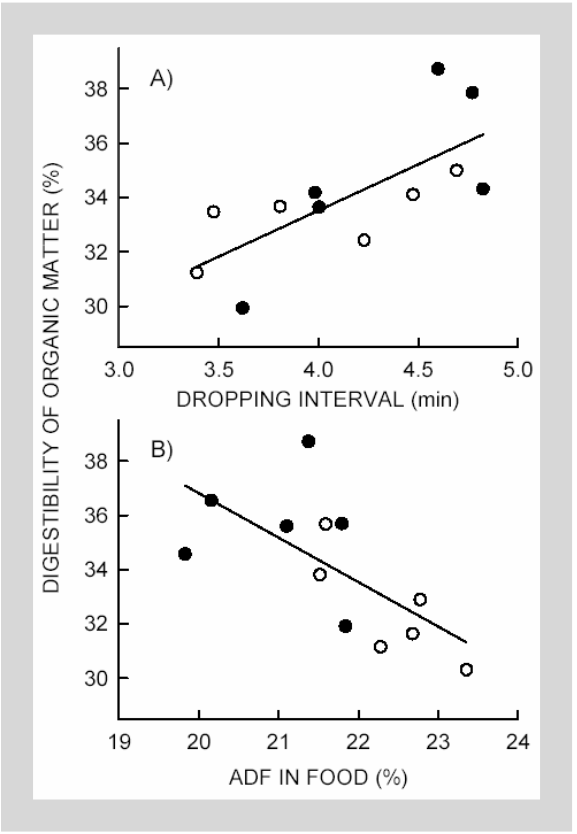


Figure 1. Relationships between the apparent digestibility of organic matter and dropping interval (A) and ADF content of the food (B). Separately indicated are trials with *Festuca* (○) and *Poa*/*Lolium* (●). Given are partial plots in which the effect of the other independent variable has been removed. Statistics are given in Table 2.

0.0005), and failed to detect more subtle changes within each plant species separately ($F_{1,9}$ = 1,8, P = 0.22). It seems that the digestibility of the nutritional components varied due to other factors and that this prevented accurate predictions of the digestibility of the food.

In a second test, we analysed the predictive power of the retention time, as measured by dropping intervals, in combination with the proximate composition of the food. By incorporating retention time in the regression we were able to allow for better digestion when food is retained for longer periods in the digestive tract (Van Soest 1982). After backward elimination of non-significant terms in the model, the apparent digestibility of organic matter appeared to be closely related to a combination of the concentration of ADF in the food and the retention time ($r^2 = 0.74$, $P < 0.01$; Fig. 1). The concentrations of protein and NDF did not contribute significantly to the final model (Table 2). Neither was plant species included in the model, indicating that the differences between species were adequately explained by the retention time and the concentration of ADF in the food. Similarly, the apparent metabolisability was closely related to the ADF concentration in the food and the retention time (see Table 2).

Field trials

The quality of the food ingested during the field trials declined during the spring with a decrease in the protein content of *Festuca* and an increase in the ADF (Table 3). Concurrently, the food was less well digested as the season progressed with a rapid drop in the digestibility of organic matter during the last two trials in April. Increases in the total food intake reflected the increasing day length available for feeding.

The observed apparent digestibility of organic matter in *Festuca* was compared with predicted values based on the results of the indoor trials (see Table 2). The predictions gave a good fit during the first five observation days ($r^2 = 0.76$) but during the last two the observed digestibilities dropped well below the predictions (Fig. 2).

Table 2. Multiple regression analysis of the apparent digestibility and metabolisability of organic matter (in %) in relation to the content in the food of protein, NDF and ADF (in % of organic matter) and to the retention time (dropping intervals in minutes). Plant species and test bird are dummy variables. Test bird, though not significant, was included in the final model. Coefficient estimates (± 1 SE) are given for an averaged individual.

	Apparent digestibility			Apparent metabolisability		
	Coefficient	t	P	Coefficient	t	P
Protein	-	-0.88	n.s.	-	-0.58	n.s.
NDF	-	0.89	n.s.	-	1.11	n.s.
ADF	-1.64 ± 0.65	-2.52	<0.05	-1.81 ± 0.68	-2.77	<0.05
Dropping interval	3.11 ± 1.19	2.33	<0.05	3.95 ± 1.40	2.81	<0.05
Plant species	-	1.42	n.s.	-	1.88	n.s.
Test bird	-	0.86	n.s.	-	1.40	n.s.
Constant	56.68 ± 18.82	2.88	<0.05	57.68 ± 19.82	2.84	<0.05
Model	$F_{3,8}$ = 7.46		0.01	$F_{3,8}$ = 9.42		0.005

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Table 3. Results of seven field feeding trials averaged for two individual barnacle geese. Given are the food composition (protein and ADF in % of the organic matter of *Festuca*), the apparent digestibilities (in % of organic matter), the total food intake per day (in g dry weight day^{-1}) and the average dropping intervals (in minutes).

Date	Protein	ADF	Apparent digestibility	Intake	Dropping interval
9 March	30.0	16.2	44.2	45.9	4.42
16 March	30.2	16.7	41.2	40.0	3.98
22 March	31.3	16.7	42.1	87.2	4.29
30 March	27.6	16.7	42.6	84.0	4.50
7 April	29.8	19.3	40.2	88.2	4.10
14 April	29.2	19.0	36.6	89.9	5.06
19 April	25.6	20.5	33.4	74.5	5.48

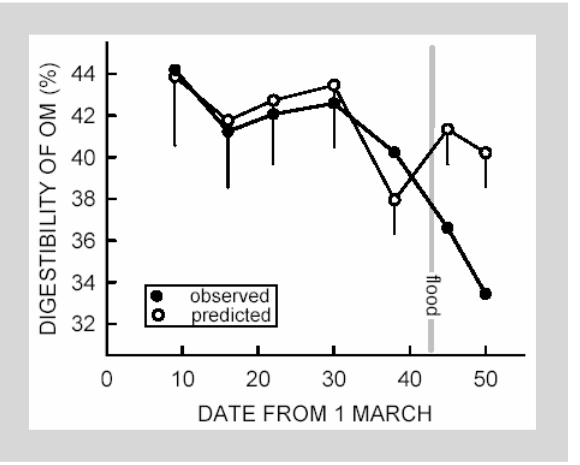


Figure 2. Apparent digestibility of organic matter of barnacle geese in large pens on *Festuca* swards. Observed digestibilities, based on ADF as a natural marker, are compared with predictions from indoor feeding trials (mean -1 SE, based on the regression in Table 2). The vertical line indicates when the salt marshes were flooded during high tides.

Discussion

Behaviour of the geese

The value of feeding trials depends on the avoidance of anomalies arising from keeping the subject animals on unnatural foods (Sibly 1981), and on their adequate acclimatisation to the experimental situation (Sedinger et al. 1989). The geese used in our trials were caught only a few months in advance; they were kept in a holding pen with a sward composed of grasses which they would have encountered in the wild; and they appeared to behave naturally during the experiments. We are confident, therefore, that their digestive systems functioned normally during the trials, and that the measured variation in digestibilities reflected a natural response to the food on offer.

Although the geese in both trials had ample food available to them, those used in the indoor experiments fed for only part of the day. It seemed that they were ingesting the minimum amount of food necessary to maintain a constant body mass. This behaviour was in contrast to that of geese in the wild at this time of the year, when they accumulate body stores by maximal ingestion of food (Owen 1980). Because the retention time of the food in the geese used in the indoor trials is likely to have been affected by this submaximal ingestion, care must be exercised when extrapolating the results to birds in the wild.

Variation in digestibility

The retention time of the food varied with two factors. First, it increased with high protein (and low cell wall) concentration. This is surprising because in several animal taxa the reverse trend is common and more food is ingested, which is processed at higher rates, if its digestibility is high (Van Soest 1982, Beckerton & Middleton 1983). Retention times are thus adjusted to the time required to digest the food, which seems an appropriate strategy when animals maximise the metabolisable energy intake. On the other hand, Foley & Cork (1992) argued that small herbivores retain low quality food for shortest periods in order to clear the digestive tract for higher quality items. This strategy applies to animals that have a fair chance to find better food in the near future which was obviously not the case for the geese during the digestion trials. Instead, it seems that the geese during the trials adopted a strategy of ingesting an amount of food that enabled them to satisfy their minimum energy needs. This is consistent with the constant body mass during the trials (see above), and also with the positive relationship between retention times and protein concentration in the food.

The second factor with which retention time varied was the day length available for feeding. This corresponds to the seasonal pattern in retention times observed in wild geese (Prop & Vulink 1992) and supports the postulate that retention time is adjusted according to day length (Prop & Vulink 1992), rather than to food quality alone (Van Soest 1982).

Longer retention times had a positive effect on the digestibility of organic matter which was also influenced by its chemical profile, in particular by the concentration of ADF. These feeding trials, therefore, confirm observations in wild geese (Prop & Vulink 1992), and in herbivores in general (Van Soest 1982, Robbins 1993), that digestion varies with food quality and retention time. The two test foods differed in the apparent digestibility of organic matter, but these differences were explained by their proximate composition. This indicates that the chemical profile of the food plants and the retention time

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together were adequate predictors of the digestibility of organic matter (see Fig. 1), and likewise of the metabolisability of energy.

The regression method

It is tempting to try to predict how well herbivores digest their food on the basis of the chemical profile of the food plants alone, without the extensive measurements necessary to determine the digestibility from food and faeces (Van Soest 1982). During the field trials we found that the digestibilities of organic matter predicted from the indoor trials fitted the observed values well. It should be noted, however, that, the significance level of the correlation may have been inflated to some extent because both the predictions from the regression and the field estimates were partly based on the ADF concentration in the food. Digestibilities were poorly predicted for the last two field trials. Immediately before these observations were made, high tides flooded the *Festuca* marshes where the trials were conducted. As a consequence of mud and salt deposited on the leaves, the food plants contained almost twice as much ash as they did during the previous trials (15.6 ± 4.6 and 8.1 ± 1.9%, sand excluded; $F_{1,5} = 15.6$, $P < 0.025$). Barnacle geese avoid food containing more than 5% salt (Canters 1973) and, assuming that most of the additional ash measured during the last two trial days (7.5%) was composed of salt, this threshold was well exceeded. In fact, we observed that wild barnacle geese avoided the parts of the salt marsh that had been inundated by moving to areas above the tide line (see also Stahl et al. 2002). Canada geese *Branta canadensis* grow at a low rate when their drinking water is highly saline (Stolley et al. 1999) and high concentrations of salt in their food impair microbial activity in the guts of sheep *Ovis aries* (Clarke 1977), suppressing food digestion. We suggest that the low digestibilities observed during the last two field trials were caused by high salt concentrations in the food plants.

The regression method is particularly useful in the analysis of feeding trials where the test diet is composed of several plant species, the digestibility of each of which is required to be measured separately. As an example, we present a case of brent geese foraging on salt marshes in the Wadden Sea in spring. Samples of food plants and of the droppings of wild geese were collected as in the field trials of our study, and the apparent digestibility of organic matter was calculated in the same way, using ADF as a marker (Prop & Deerenberg 1991). To model food selection, it is necessary to know the digestibility of each plant species separately. This can be achieved by predicting the digestibility or metabolisability of organic matter from the regression models generated in this study (see Table 2). The four food species varied widely in their digestibility (Table 4) and this would have been difficult to show without using the regression method. As a further check on the validity of the method, the average digestibility of this sample was calculated from the four digestibilities weighted by their importance in the diet. This weighted mean of the apparent digestibility of organic matter was close to the estimate of digestibility obtained using ADF as a marker (38.5 and 37.3%, respectively), as was the case in all of the samples collected in the brent goose study (36.9%, SE = 0.77 and N = 50, compared to an average of 35.3%, SE = 0.88, with the marker method, with a correlation coefficient of 0.76).

In conclusion, predicting the digestibility of food on the basis of regression models generated from feeding trials may provide good estimates in a cost-effective way. One pitfall of such an approach, however, is that unexpected factors may become important. We were faced with sudden increases in the concentration of salt in the food during the field tests which we think impaired its digestion. Similarly, high concentrations of secondary plant compounds (tannins, for example) may cause a less efficient digestion than might be expected on the basis of nutrient components alone (Robbins 1993). We do not, therefore, advocate the regression method as a replacement for the marker technique, but suggest that predicting the digestibility of organic matter from regressions is particularly useful when estimating the individual nutri-

Table 4. Apparent digestibility (in % of organic matter) for each of four plant species ingested, based on ADF in the plants (in % of organic matter) and on an average dropping interval for the date of collection of 4.25 minutes. Calculations followed the regression model in Table 2. The digestibility of the sample weighted by the importance of each of the species in the diet (in %) was close to the estimate obtained using the marker method (bottom line). This example was extracted from a study on brent geese (Prop & Deerenberg 1991).

Plant species	In diet	ADF in plants	Apparent digestibility
Festuca rubra	3.0	21.2	35.2
Puccinellia maritima	17.8	16.6	42.7
Plantago maritima	69.1	20.5	36.4
Triglochin maritima	10.0	14.9	45.5
Weighted apparent digestibility (% of om)			38.5
Apparent digestibility using a marker (%)			37.3

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tional value of different food plant species in mixed diets. Knowledge on the digestive physiology of herbivorous waterfowl is limited (Sedinger 1997), and in particular understanding variation in the ability to digest food among waterfowl species is an underdeveloped field of study (Bruinzeel et al. 1997). More work is therefore needed to validate and to refine the regression models generated in this study, and to make it applicable to a wide range of herbivorous waterfowl.

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