

Faecal nitrogen: a potential indicator of red and roe deer diet quality in forest habitats

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A b s t r a c t. The relationship between faecal nitrogen (FN), dietary nitrogen (DN) and dietary metabolizable energy (DE) was studied in two localities in the region of the Jeseníky Mts, Czech Republic, during four seasons. The content of nitrogen in plants significant for nutrition ranged between 0.99 and 3.86 g/kg of dry matter and DE was from 7.8 to 10.7 MJ/kg of dry matter. The DN/DE ratio in individual plant species ranged from 1:2.49 (stinging nettle) to 1:9.05 (rowan). The content of nitrogen in vegetation samples correlated with the content of DE in all four seasons ($p < 0.01$). In both the red and roe deer the diet contained more DN and DE during the vegetation season (spring to autumn) than in winter. The content of FN corresponded to the changes in diet quality and was positively correlated with DN and DE contents in all cases. On the basis of the correlations found between FN and diet quality we conclude that the use of FN for evaluation of diet quality in ungulates is possible, on the condition that we know the composition of their diet in the studied environment. However, it is unwise to compare different feeding specialists or individuals of one species living in different habitats with different diet composition.

Key words: free-living ungulates, faecal indicators, monitoring diet quality

Introduction

Herbivore populations all over Europe have been strongly influenced by human activities. A combination of harvest, changes in forest structure, supplementary feeding, predator extirpation and others factors have led in most cases to increases of their populations and a severe impact on the composition and structure of the forest vegetation over the last 30 years. Heavy deer browsing has often been considered an important factor in preventing the natural regeneration and stability of forest ecosystems (G i l l 1992a, 1992b). There is therefore a continued research effort on the effects of deer feeding behavior on the state of vegetation.

Effective management of ungulate populations and of forest ecosystems should be based not only on detailed information about the impact of deer browsing and the number of deer to harvest but also on the density of deer species, the food supply, the structure of diets consumed by individual species, attraction and quality of the individual components of food supply and the total quality of food taken. Easily applied methods to obtain reliable information are essential.

The study of the composition and quality of diets of free-living ungulates is important for understanding their feeding motivations but is complicated due to difficulties with sample collection, lack of accurate data on nutritional value of individual plant species and high costs of chemical analyses. Many problems associated with the collection of material can be solved by using faeces, which are routinely used to determine the plant composition of the diet from the undigested residues (D e J o n g et al. 1995, C o r n e l i s et al. 1999, H o m o l k a & H e r o l d o v á 2001). The possibility of estimating the nutritional value

of herbivore diet is very attractive. The main advantage of this method is that there is no need to perform feeding experiments or to kill animals and therefore it is possible to obtain sufficient material from free-living species outside of the hunting season. The quality of the food taken is estimated according to the contents of indicators which correlate with diet quality. The most frequently used diet quality indicator is faecal nitrogen (FN), which is easy to determine and is considered to have a good relationship to diet quality of herbivores. A correlation of FN with the diet contents of nitrogen, fibre and metabolizable energy has been proven in both domestic and wild animals (Leslie & Starkey 1987, Hodgman et al. 1996, Kucera 1997). Despite being used as a predictor of diet in herbivores for more than 20 years, this technique has still not been generally accepted (Hobbs 1987). The limitations of FN are through number of factors influencing its values. FN is a combination of unabsorbed dietary, undigested microbial and endogenous nitrogen. The main problem is the unabsorbed nitrogen because it is dependent on the concentration of DN and its digestibility, which can be strongly reduced by antinutritive compounds, especially tannins. This effect can complicate the comparison of diets with different botanical composition, as a high quality diet with high level of nitrogen can also have high digestibility, while a low quality diet with antinutritive compounds can have low digestibility, and the values of FN will be similar (Hodgman et al. 1996, Min et al. 2003).

Despite these possible complications, estimating the diet quality of herbivores via FN is very attractive and can help in a study of feeding strategy of free living ungulates. In this study we tried to clarify the reliability of FN for estimating deer diet quality and the conditions that enable us to use this technique in the forest environment. We tested the relationship between FN and two diet quality parameters in red and roe deer in a typical forest environment of the Czech Republic, the Jeseníky Mts. Quality of diet was estimated on the basis of dietary nitrogen (DN) and dietary metabolizable energy (DE). These parameters are accepted as the most limiting currencies for large herbivores (Robbins 1993). Recent results suggest that herbivores have the ability to select their food according to both its energy and protein content and that the importance of the content of digestible energy is much higher than that of nitrogen (Provenza et al. 1996, Villalba & Provenza 1997, Berteaux et al. 1998). However, the content of DN is closely correlated with DE in most natural forages (Westoby 1974, Owen-Smith & Novellie 1982) and has been shown to be a simple but effective indicator of the nutritive quality of ruminant diets (Staines et al. 1982, Latham et al. 1999).

Study Area

The data were collected from September 1999 to June 2001 in the central part of the Hrubý Jeseník Mts (northeast of the Czech Republic) at two sites:

1. Praděd Mt. (PD) at altitudes of 1300–1490 m a.s.l., covered with subalpine meadows and natural spruce forest. The vegetation on the subalpine meadows comprised mostly grasses and rushes (80% of the cover). Some 18% of the cover was wavy hair grass, 15% blueberry; cover of dicotyledonous herbs was low (<1%). In the shrub layer there was only spruce. The natural spruce stands were a virgin formation with individuals of various ages up to 270 years, with a little admixture of rowan (*Sorbus aucuparia*) in both tree and shrub layers. The mean cover of the herb layer was 75% with dominant blueberry (28%); the cover of grasses was 11% in total.
2. Karlova Studánka (KS) at altitudes of 700–900 m a.s.l. was covered with secondary spruce stands and remains of beech stands, with an admixture of sycamore, and was about 3 km from

the Praděd Mt. The spruce stands of 15–70 years were mostly without undergrowth. In older stands there was spruce in the shrub layer, while broadleaved species were present only sparsely (less than 5%). Wavy hair grass was significantly represented in the herb layer (33% of the cover). The clear-cut areas were mostly covered with grasses of the genus *Calamagrostis*.

The area of each of the two localities was about 500 hectares. During the vegetation season, red deer and chamois and sporadically also roe deer were present at Praděd Mt. In winter, most of the red deer migrated 2–10 km to lower locations, including the site KS, and a smaller group moved down from the summit clearings to places under the lower edge of the area on the border of the natural and secondary spruce stands (around 1100 m a.s.l.). At the site KS, red and roe deer were present all year round. However, most of the red deer left the area in spring and moved to higher locations.

Material and Methods

During four seasons of the year (spring = May, summer = July, autumn = September and winter = November to January) we collected samples of vegetation and faeces at both localities. Only samples of those plants whose share in the diet was over 1% were collected. We picked those parts of plants that the deer usually browse (simulation of browsing) and we took at least 5 samples of each species. Samples of fresh faeces were collected at the same times as the vegetation samples and from each species we obtained a minimum of 10 samples. At the site PD we collected faeces of red deer and at the site KS faeces of both red and roe deer. The samples of vegetation and faeces were dried in a ventilated drying chamber at 60°C to constant weight.

Diet composition

The seasonal composition of the diets consumed by red and roe deer was investigated with microscopic analyses of plant remains in their faeces. In evaluating the overall character of the diet, the components were pooled to form primary forage classes: grasses, *Rubus* spp., browse (leaves and shoots of broadleaved trees), bilberry, needles, forbs and ferns.

Quality of diet and faeces

We assessed the content of Kjeldahl nitrogen in both vegetation and faeces and also, in the vegetation, the content of crude protein, fat, fibre, nitrogen free extract (NFE) and ash. On the basis of nutritional characteristics we calculated the content of metabolizable energy in the main diet components (Sommer 1994) using the Axelsson's regression equation to assess the content of digestible organic matter and the regression equation according to McDonald et al. (1988) to calculate the content of digestible nitrogen compounds. We then calculated the contents of nutrients in the whole diet according to Westoby (1974) or Leslie et al. (1984).

Statistics

The differences in the average volume of the diet components between individual seasons were tested with one way ANOVA and a subsequent Pos hoc test (Bonferroni). Prior to evaluation, the data were modified by angular transformation (Sokal & Rohlf 1981). The relationship between the content of nitrogen and ME in the diet components was

determined using Spearman rank correlation. The differences in the contents of individual diet quality indicators were tested with ANOVA.

Results

Botanical composition of diets of red and roe deer

Grasses prevailed (about 80%) in the diet of red deer at the KS in summer and autumn and were consumed more than in spring and winter (about 30%; $p < 0.05$). Shoots of broadleaved woody species and needles dominated the diet of red deer in winter and spring, and there were almost equal amounts of grasses, dicotyledonous herbs and broadleaved woody species (Fig. 1).

Roe deer consumed mostly *Rubus* spp. from spring to autumn (80–90%). In winter, needles and broadleaved woody species predominated. Other components in total did not exceed 10% of the volume of food.

At the site PD grasses formed the main part of red deer diet all year round (80–90%); other components were consumed in limited amounts only (less than 5%; Fig. 1).

Quality of consumed plant species

The content of nitrogen in individual plant species varied between 0.99 and 3.86 g/kg of the dry matter and DE between 7.8 and 10.7 MJ/kg of the dry matter (Fig. 2). The average concentrations of DN and DE were generally highest in spring and summer and lowest in winter. During the vegetation season the content of nitrogen and DE was the highest in forbs and foliage of woody species, the lowest in grasses. In winter the highest nutritional value was found in blackberry.

The DN/DE ratio in individual species ranged from 1:2.49 (stinging nettle) to 1:9.05 (rowan). Significant correlations between DN and DE in plants from the same season were found in approximately half of the cases (Table 1, Fig. 2), but in all of the cases in plants that served as the main food sources ($p < 0.01$).

Diet quality and faecal nitrogen

The quality of diets of red and roe deer in the individual seasons varied. In both species it contained more DN and DE in the vegetation season than in winter. The content of FN

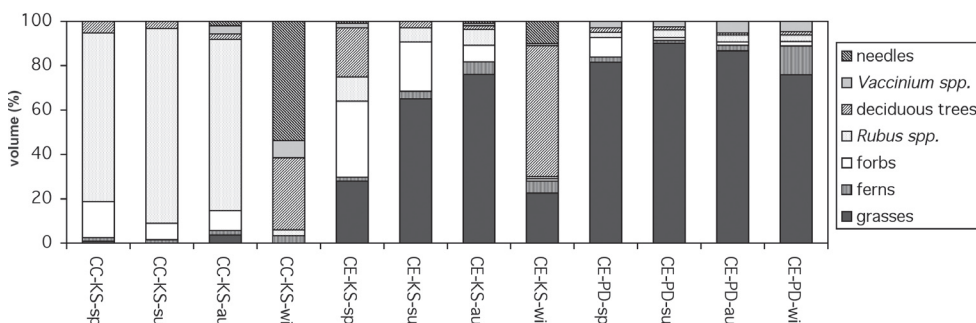


Fig. 1. Composition (% volume) of the red (CE) and roe (CC) deer diet in spring (sp), summer (su), autumn (au) and winter (wi) in locality Pradéd (PD) and Karlova Studánka (KS).

corresponded to the changes of diet quality and was in positive correlation with the contents of DN and DE in all cases (Figs 3, 4).

The content of FN in the diets of the studied species varied. According to this indicator, the diet quality during the vegetation season (spring to autumn) was higher in roe deer than in red deer at both localities. In winter the content of FN in roe deer was lower than in red deer. In both species at both localities the content of FN was higher in the vegetation season than in winter. The content of FN in the individual seasons was the highest in roe and red deer at the KS in spring and in red deer at the PD in autumn (Figs 3, 4.).

The relationship between FN and DE at the PD in the samples from red deer was less close than in the same species at the KS and also the slope of the regression line was lower in these cases than in the samples from the site PD.

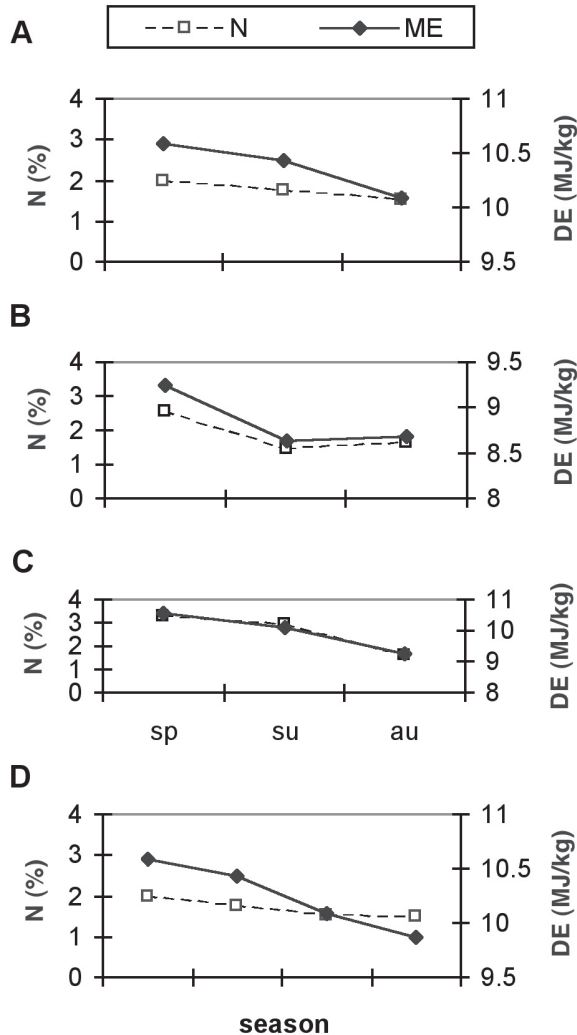


Fig. 2. Content of nitrogen (N) and energy (DE) in the most important diet components and in the diet of red and roe deer: blueberry (A), wavy hair grass (B), raspberry (C), reed grass (D), diet of red deer (E), diet of roe deer (F) of Jeseníky Mts during individual seasons of the year (sp, su, au, wi).

Table 1. Content of faecal nitrogen (FN), dietary nitrogen (DN) and dietary metabolizable energy (DE) in red (CE) and roe deer (CC) in spring (sp), summer (su), autumn (au) and winter (wi) in locality Praděd (PD) and Karlova Studánka (KS). Different numbers distinguish differences ($P < 0,05$) between deer species in a frame of individual seasons (for example the content of FN between CE-PD and CE-KS in spring was different – 1 x 2) and different letters distinguish the one between season in a frame of species (for example the content of FN between CE-PD in all seasons was different A x B x C x D).

season	category	FN	DN	DE
sp	CE-PD	¹ 3.74 ± 0.26 ^A	¹ 2.76 ± 0.32 ^A	¹ 9.94 ± 0.32 ^A
	CE-KS	² 3.73 ± 0.25 ^A	¹ 2.85 ± 0.33 ^A	² 10.11 ± 0.27 ^A
	CC-KS	³ 3.97 ± 0.05 ^A	² 3.13 ± 0.19 ^A	³ 10.35 ± 0.12 ^A
su	CE-PD	¹ 2.92 ± 0.24 ^B	¹ 2.24 ± 0.25 ^B	¹ 9.64 ± 0.34 ^B
	CE-KS	² 3.04 ± 0.17 ^B	² 2.38 ± 0.18 ^B	² 9.77 ± 0.32 ^B
	CC-KS	³ 3.17 ± 0.11 ^B	³ 2.48 ± 0.09 ^B	³ 9.98 ± 0.27 ^B
au	CE-PD	¹ 2.42 ± 0.28 ^C	¹ 1.82 ± 0.19 ^C	¹ 9.55 ± 0.38 ^B
	CE-KS	² 2.57 ± 0.22 ^C	² 1.94 ± 0.12 ^C	² 9.74 ± 0.32 ^B
	CC-KS	³ 2.71 ± 0.21 ^C	³ 2.01 ± 0.14 ^C	³ 10.01 ± 0.21 ^B
wi	CE-PD	¹ 1.62 ± 0.19 ^D	¹ 1.51 ± 0.16 ^C	¹ 8.67 ± 0.54 ^B
	CE-KS	² 1.52 ± 0.15 ^D	² 1.42 ± 0.09 ^D	² 8.34 ± 0.30 ^C
	CC-KS	³ 1.47 ± 0.14 ^D	³ 1.49 ± 0.06 ^D	³ 8.13 ± 0.22 ^C

Discussion

Faecal nitrogen has often been considered to be a good indicator of the diet quality of free living ungulates (Blanchard et al. 2003, Kamlér et al. 2003, Irwin et al. 1993). In several studies correlations have been found between FN and DN (Leslie & Starkey 1985, Howerly & Pfister 1990, Hodgman et al. 1996) and between FN and DE (digestible organic matter, metabolizable energy, digestive energy) (Holloway et al. 1981, Holeček et al. 1982, Hodgman et al. 1996). Although these studies have verified the relationship of FN to diet quality parameters in several ungulate species, areas and seasons, there have still been some doubts about its reliability. On that account it is necessary to precisely evaluate the conditions affecting FN values and its reliability in specific areas. Our results are in agreement with findings confirming the close relationship of FN to diet quality. In our study FN generally indicated diet quality well in both red and roe deer and correlated with differences in the diet between deer species, seasons and areas.

The clusters of points (Figs 3, 4) that are connected with the regression line are less distinctive at site PD than KS, where the values from winter and spring are markedly separated from those of summer and autumn. In the material from PD the points are dispersed more evenly. This fact may indicate that the relationship between FN and diet characteristics can be influenced by some factors characterizing the biotope. On the contrary, the difference (value r , tangent of the regression line) in the relationship between FN and diet quality indicators was the same in both roe and red deer within one site. This indicates that the applicability of this method is independent of the herbivore species and its feeding specialization. This corresponds with results obtained in species with different feeding types, for example bighorn sheep (Irwin et al. 1993), mule deer (Kucera 1997), and sika deer (Asada & Ochiai 1999).

Values of FN were the best predictor of dietary nitrogen ($r^2 = 0.82 - 0.93$; $p < 0.001$ in all of the cases) but were closely correlated also to dietary energy. However, the dynamics of FN, DN and DE showed some disproportions in the autumn and in winter that may have

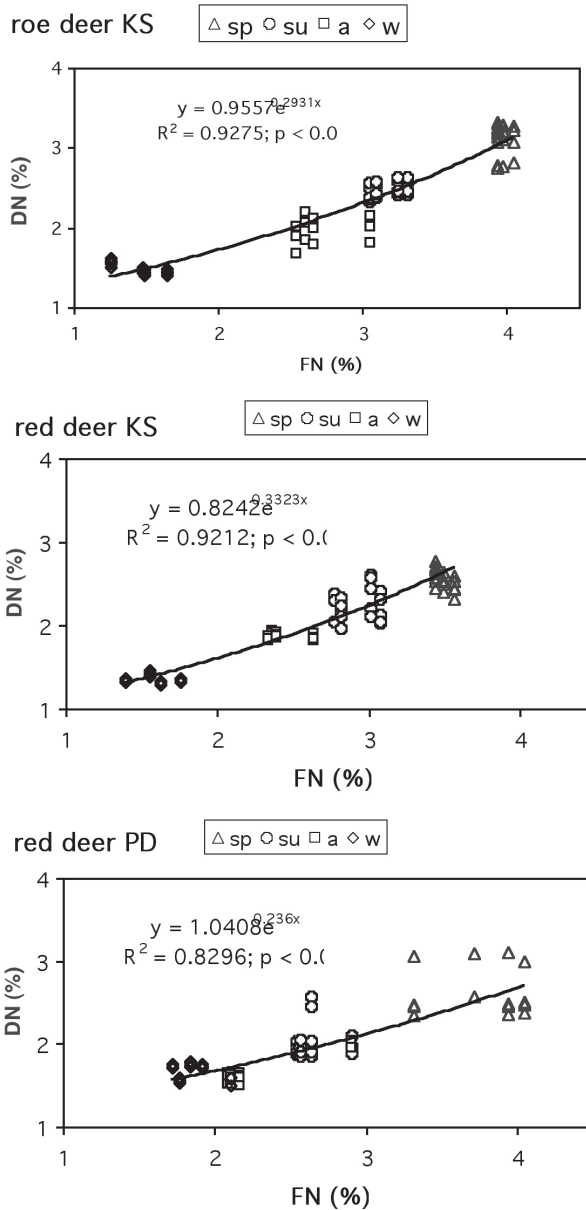


Fig. 3. Correlation between faecal nitrogen (FN) and dietary nitrogen (DN) in red and roe deer in locality Pradč (PD) and Karlova Studánka (KS) in spring, summer, autumn and winter.

been caused by the changes in DN/DE ratio or by the content of antinutrition substances that influence the digestibility of proteins (H o b b s 1987). Nitrogen content in our deer diet ranged from 1.5% to 3.1% and can be considered as sufficient as it corresponds to data from other environments (L e s l i e et al. 1984 – 1.3–3.4% in red and black-tailed deer, H o d g m a n et al. 1996 – 0.96–2.9% in black-tailed and mule deer, L a t h a m et al. 1999 – 1.5–3.0% in red and roe deer) and exceeds the minimum nitrogen content used in feeding

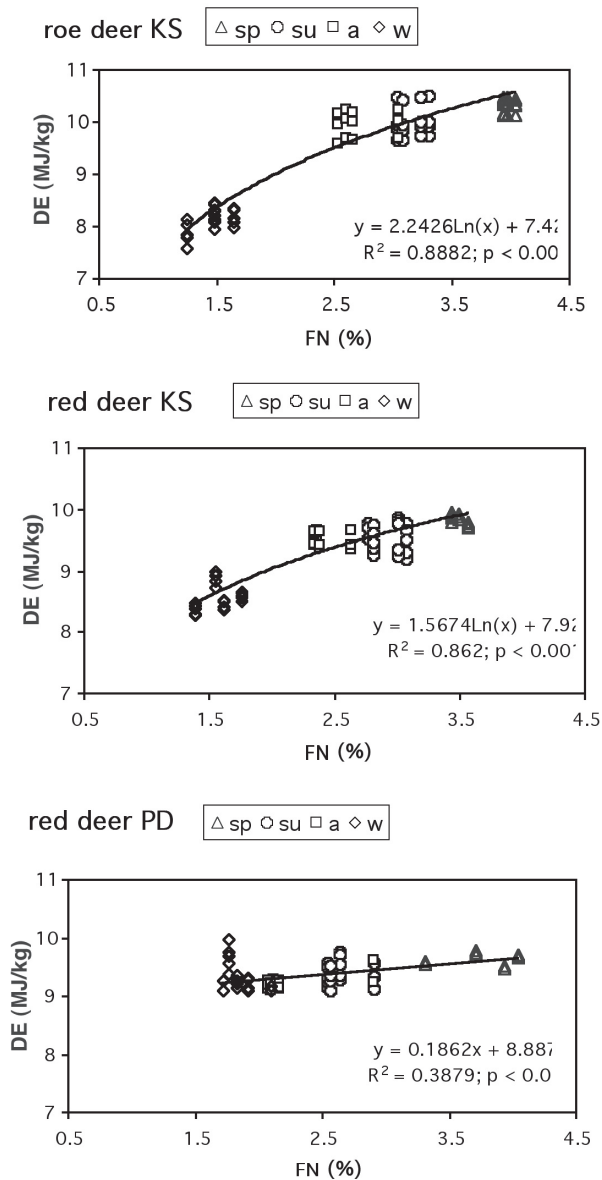


Fig. 4. Correlation between faecal nitrogen (FN) and dietary energy (DE) in red and roe deer in locality Praděd (PD) and Karlova Studánka (KS) in spring, summer, autumn and winter.

experiments (Mould & Robbins 1981, Brown et al. 1995, Asleson et al. 1997). Therefore, nitrogen was not the limiting nutrient even in winter and for deer the content of dietary energy is probably more interesting. The selection of a diet higher in energy but lower in protein was determined by using experimental foods in free living white-tailed deer in Canada. In this experiment nitrogen levels ranged from 1.8 to 2.6% and deer were able to discriminate between experimental foods and preferred foods higher in digestible energy or at each given level of digestible energy the foods lower in nitrogen (Berteaux et al. 1998).

The quality of the herbivore diet is determined especially by dietary energy, but the faecal nitrogen used as its indicator is dependent especially on dietary nitrogen. The two most important factors influencing the accuracy of FN as a quality indicator are: 1. the nitrogen/energy ratio and 2. antinutritive compounds.

The nitrogen/energy ratio in all plant species we analyzed ranged from 1:2.5 to 1:9. We tried to calculate theoretical simple summer diets in our upper and lower site. At the upper site it was composed of 80% wavy hair grass and 20% rowan (8.9 MJ DE, 1.8% N and N/DE 1/4.7) and at the lower site of 70% raspberry, 20% stinging nettle and 10% greater stitchwort (9.1 MJ DE, 2.8% N and N:DE 1/3.2). Both diets have similar contents of DE (2% difference), but the content of dietary (and probably faecal) nitrogen differs by 35%. This example shows one factor which limits the use of nitrogen as a diet quality indicator.

Another important limitation is differences in nitrogen digestibility. This factor is not so important between different animal species (in our material there were only minor differences between red and roe deer) but nitrogen digestibility can be strongly affected by antinutritive compounds, especially tannins. Generally the digestibility of low quality diets with low energy content is lower than that of high quality diets. Hodgman et al. (1996) fed mule deer with forage of different qualities and found nitrogen digestibility of 73% when its content in the diet was 17% (this corresponds to 4.6% of nitrogen in faeces) and digestibility of 15% when its content in the diet was 7% (this corresponds to 6% of nitrogen in faeces). Differences of FN in this case were inconspicuous despite great differences in diet quality.

Conclusion

Our results confirm the relationship between the content of nitrogen in faeces and diet quality in herbivores. When we use FN as an indicator of diet quality of large herbivores we have to consider relatively similar DN/DE ratios and the content of tannins in their diet. The use of FN for evaluation of the diet quality in ungulates is possible especially in long-term studies when the botanical diet composition is stable. The comparison of diet quality of different feeding specialists with great differences in food choice, or individuals of one species but from different environments with different diet compositions, remains a problem.

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