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ORIGINAL PAPER

Evaluation of winter food quality and its variability for red deer in forest environment: overwintering enclosures vs. free-ranging areas

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Abstract

Populations of European ungulates have grown substantially over recent decades, resulting in considerable environmental and socio-economic impacts. Availability and quality of natural and supplemental food sources are among the main factors driving their population dynamics. Detailed knowledge of food quality of management-targeted species is therefore of primary importance for their successful management. The main aim of this study was to evaluate winter food quality and its variability for an important ungulate species in the Czech Republic - i.e. red deer, using faecal indices (faecal nitrogen, faecal acid detergent fibre, faecal neutral detergent fibre) and near infrared reflectance spectroscopy. We compared food quality for red deer and its possible differences between overwintering enclosures (i.e. fenced areas where red deer spend harsh winter conditions) and neighbouring unfenced free-ranging areas within two study areas. The results obtained showed that winter food quality and its variability for red deer are of different quality and variability in the overwintering enclosure and neighbouring free-ranging area. The observed differences in concentrations and amounts of variation of faecal indices are most probably related to animal densities at individual study areas. Wildlife managers should therefore keep animals in overwintering enclosures at moderate densities and to provide high quality forage to all individuals in order to balance nutrition of both the individuals inside and outside the enclosures. Nevertheless, further studies are needed in order to provide deeper knowledge on red deer food quality and its variability in space and time.

Key words: deer diet; nutrition; near infrared reflectance spectroscopy; nitrogen; fibre

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1. Introduction

Numbers of free-ranging ungulates have been recently increasing throughout the whole Europe (Apollonio et al. 2010). These overabundant ungulate populations may have significant impacts on the structure and functioning of their environment, resulting in considerable economic losses in agriculture and forestry (Weisberg & Bugmann 2003; Côté 2004; Massei & Genov 2004). Food quality and availability are among the main factors determining condition, survival and reproductive success of free-ranging ungulates, as well as one of the main driving forces influencing their distribution and habitat selection (Pettorelli et al. 2003; Parker et al. 2009; Van Beest et al. 2010). Accordingly, detailed information on food quality for large ungulates is essential for their efficient management.

Red deer (*Cervus elaphus*) feed opportunistically on mixed diet of grass and concentrate food items such as browse, forbs and fruits (e.g. Gebert & Verheyden-Tixier 2001; Krojerová-Prokešová et al. 2010). Food quality (i.e. in terms of the content of nutrients, digestible energy and digestibility-reducing compounds) is of particular importance to red deer (Robbins 1993; Van Soest 1994). They do not simply consume any plant species they encounter, but demonstrate preferences for plant species containing higher amounts of nitrogen and digestible energy and lower amounts of digestibility-reducing substances, such as fibre and secondary metabolites (e.g. Robbins 1993; Forsyth et al. 2005; Iason 2005).

Direct measurements of food quality for herbivorous ungulates can be both time-consuming and expensive (Leslie et al. 2008). An alternative approach is to measure a nutritional characteristics of faeces that bear a relationship to the quality of ingested diet (Holechek et al. 1982a; Leslie & Starkey 1985). Faecal material offers a convenient, non-invasive method as it is readily available and easy to obtain. There are several faecal constituents demonstrating the relationship with food quality of herbivorous ungulates (Belovsky 1981; Robbins 1993). Among the most widely applied faecal indices of food quality are faecal nitrogen (FN), faecal acid detergent fibre (FADF), and faecal neutral detergent fibre (FNDF; Leslie et al. 2008; Dixon & Coates 2009). Despite its broad application, the use of FN as an indicator of food quality for ungulates remains controversial (see review by Leslie et al. 2008). The digestibility of the diet affects the FN levels as the bacterial fermentation activity as well as turnover increases with higher digestibility (Robbins 1993). This results in a positive linear relationship between digestibility and FN (Holechek et al. 1982b). Since nitrogen content shows a positive linear relationship with digestibility in plants, FN also correlates with dietary nitrogen, which is one of the most important parameters of food quality for herbivorous ungulates (e.g. Robbins 1993; Leslie & Starkey 1985; Hodgman et al. 1996). However, woody plant species contain secondary

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metabolites which are known to bind with plant proteins and gastrointestinal enzymes during chewing and digestive processes. These complexes are not digestible at rumen pH and are excreted in the faeces, thereby inflating concentrations of FN (Robbins 1993; Palo & Robbins 1991). Nevertheless, it has been suggested that under natural conditions, where free-ranging herbivores can make their own choice of what plant species they will consume, a relatively consistent correlation exists between FN and dietary nitrogen (Palo & Robbins 1991).

Regarding the fibre fractions in faeces, NDF consists predominantly of hemicellulose, cellulose and lignin (Van Soest et al. 1991) and it has been demonstrated that increasing levels of NDF in diet reduce voluntary food intake (Van Soest 1994). A subset of NDF is ADF, which represents lignin, cellulose and cutin – i.e. the least digestible compounds for most herbivores (Van Soest et al. 1991). As content of ADF in diet increases, digestibility as well as available energy decreases (Van Soest 1994). Red deer are known to show higher preferences for plant species containing lower levels of fibre (Forsyth et al. 2005). Adequate levels of fibre in diet are however required to maintain normal rumen function (Van Soest 1994).

Plant nutrients and thus quality of food consumed by herbivorous ungulates are highly variable in space and time (e.g. Palo & Robbins 1991; Crawley 1997; Holá 2012). To efficiently evaluate variation in food quality, however, requires large number of samples and the wet-chemistry methods used to measure FN, FADF, and FNDF in faeces frequently become very time-consuming and expensive. Near infrared reflectance spectroscopy (NIRS) provides a useful tool to overcome these drawbacks since it allows rapid, low-cost, chemical-free, and non-destructive analyses of a large number of samples (Foley et al. 1998). NIRS has been widely used in wildlife nutrition research over the past four decades and numerous studies have used NIRS to measure food quality through faecal indices in herbivorous ungulates (Kamler et al. 2004; Dixon & Coates 2009; Showers et al. 2006).

In recent decades, the use of fenced overwintering enclosures for free-ranging ungulates is a common management practice in many central European countries, including the Czech Republic. The main purpose of these enclosures is to reduce damage to forest stands and to assist animal survival over harsh winter conditions. Enclosures are 10 – 50 ha and animals are usually kept inside for about a half-year (i.e. from the beginning of December until the beginning of growing season; Putman & Staines 2004; Pepin et al. 2006). Supplementary feeding is a major food source for animals kept inside the enclosures. Therefore, temporarily confining the animals into a restricted fenced area may be reflected in their feeding habits and quality of food consumed. Considering the importance of food quality for herbivorous ungulates, it is essential to evaluate the quality of foods consumed inside the enclosures in comparison to foods consumed outside them.

Our purpose here was thus to evaluate winter food quality and its variability for red deer using faecal indices (i.e. FN, FADF, FNDF) and NIRS. We compared food quality for red deer and its possible differences between overwintering enclosures (i.e. fenced areas where red deer spend harsh winter conditions) and neighbouring unfenced free-ranging areas within two study areas in the Czech Republic. We selected winter since this time period is of particular importance for red deer. Plants available in winter are usually less digestible and have lower amounts of necessary nutrients (Van Soest 1994). Severe winter conditions and related reduction in food quality are thus among the main factors influencing survival and reproduction success of red deer populations (Christianson & Creel 2007).

2. Materials and Methods

2.1. Study areas

Faecal samples of red deer were collected during winter 2013 in two study areas in the Czech Republic: (i) military training area Hradiště (Karlovy Vary region; hereinafter MTA Hradiště), and (ii) military training area Boletice (South Bohemia region; hereinafter MTA Boletice; Fig. 1). The climatic conditions of study areas is describe in the Table 1.

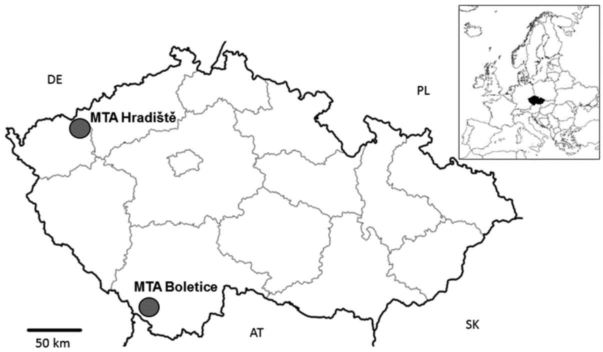

Fig. 1. Location of the study areas (indicated by grey circles) within Europe and the Czech Republic.

Table 1. Climatic conditions during winter 2013.

		January	February	March	April
Average monthly temperature [°C]	MTA Boletice	−4.2	−5.1	−3.9	4.2
	MTA Doupov	−2.8	−3.5	−2.7	6.8
Duration of snow cower [day]	MTA Boletice	28	28	25	8
	MTA Doupov	21	20	17	6

The MTA Hradiště (50°16´ N, 13°7´ E) is situated in the Doupovské hory Mountains and has a total acreage of 331 km^2. Forests cover 41% of the area, agricultural land 8%, other land cover types 51%, and water surfaces 0.2%. Deciduous forests with Norway spruce (*Picea abies*), European larch (*Larix decidua*), and pine (*Pinus sylvestris, Pinus nigra*) cover 71%. Broad-leaved forests with beech (*Fagus sylvatica*), sycamore maple (*Acer pseudoplatanus*), and ash (*Fraxinus excelsior*) cover 29%. The predominant forest type is herb-rich beech forest. The other forest types are ravine forests, alluvial forests, oak-hornbeam forests, and thermophilous oak forests (Vojta & Kopecký 2006).

The MTA Boletice (48°49´ N, 4°13´ E) has a total acreage of 219 km^2. Forests cover 60% of the area, agricultural land 10%, and shrubs and natural open areas 30%. Spruce forests with Norway spruce (*Picea abies*) and rowan (*Sorbus aucuparia*) are the dominating cover. Flowering beech forests and acidophilus beech forest mostly with European beech (*Fagus sylvatica*) and sycamore maple (*Acer pseudoplatanus*), and fir forests with silver fir (*Abies alba*) are found at altitudes between 600 and 1000 m a.s.l. Large complexes of semi natural treeless areas occur at lower altitudes.

Regarding the overwintering enclosures in our study areas in 2013, the enclosure in the MTA Hradiště had a total acreage of 12 ha with 280 individuals of red deer (90%), and sika deer (10%; *Cervus nippon*), and the enclosure in the MTA Boletice had 8 ha with 35 individuals of red deer. Supplemental feed (i.e. corn and meadow hay) was regularly provided to free-ranging ungulates, including red deer, in the overwintering enclosures and neighbouring free-ranging areas in both study areas from November to May.

2.2. Sampling and chemical analyses

We randomly collected fresh red deer faeces from fenced overwintering enclosures and neighbouring unfenced areas within each study area during winter 2013 (n = 149 in MTA Hradiště, n = 161 in MTA Boletice). All faecal samples were oven-dried to constant weight at 50 °C and subsequently ground to pass 1 mm sieve.

A subset of faecal samples (i.e. calibration (n = 100), further used for NIRS interpolation of chemical constituents in the remaining samples, was assayed by standard chemical methods to determine the exact concentrations of FN, FADF, and FNDF. Total FN content was determined using an automated C/N analyser TruSpec (LECO Corporation, USA) after oxygen combustion in an oven at 950 °C. Total FADF and FNDF concentrations were determined by standard methods of the Association of Official Analytical Chemists (AOAC 1984). The results of the chemical assays were then used to calibrate NIRS as described by Foley (1998). All faecal samples were scanned from1 100 to 2 500 nm using a Thermo Nicolet NEXUS 670 scanning spectrophotometer and an OMNIC 7.4 software (Thermo Scientific™, USA). The spectrum of each sample was the average of 32 successive scans at a resolution of 4 cm^{-1}. Each spectrum was recorded as the logarithm of the reciprocal of reflectance (log 1/R).

Prior to calibrations, the scatter correction of standard normal variate (SNV) and detrend was applied to the spectral data, along with a number of possible combinations of derivative (1,2), gap (4,10), and smoothing (4,10; Barnes et al. 1989). The calibrations were performed by partial least square (PLS) regressions with internal cross-validation (Shenk & Westerhaus 1991). Outliers were detected by using the residual sample variance plot after the PLS regression. The predictive ability of the PLS equations was evaluated on the basis of coefficient of determination (R^2) of the linear regression of predicted against measured values, the root mean square errors of calibration (RMSEC), the root mean square errors of cross-validation (RMSECV), and the ratio of performance deviation (RPD), which is the ratio of the standard deviation of the reference values and the root mean square errors of prediction (RMSEP). Good predictions are regarded as having an $R^2 > 0.81$ and an RPD > 2. Predictions having $0.66 < R^2 < 0.80$ and 1.5 < RPD < 2 are considered to be approximate and predictions having $R^2 < 0.65$ and an RPD < 1.5 are considered to be poor (Shepherd & Walsh 2007).

Statistical analysis

The Kendall´s tau τ correlation coefficients were calculated in order to evaluate whether there was any relationships among FN, FADF, and FNDF in individual study areas.

The amounts of individual faecal indices of food quality within and outside the overwintering enclosures in individual study areas were compared by Student´s t-tests or Wilcoxon signed-rank test depending on the normality of the data.

To quantify the degree of variation in food quality in overwintering enclosures and neighbouring free-ranging areas, the coefficients of variation (i.e. CV, standard error divided by mean) for concentrations of FN, FADF, and FNDF were estimated. Significance was tested at $\alpha = 0.05$ level. All statistical analyses were performed with the R software, version 3.1.1 (R Development Core Team, 2014).

3. Results

Overall, a total of 310 red deer faecal samples, including 149 from the MTA Hradiště and 161 from the MTA Boletice, was analysed for concentrations of FN, FADF, and FNDF.

The developed calibration models (derived from the absorbance spectra of faeces) confirmed the high potential of near infrared reflectance spectroscopy for analysing a large number of samples and accurate determination of major faecal indices of food quality for red deer (Table 2).

Table 2. Developed calibration models. Predictive power of partial least square regression with cross-validation for modelling the relationship between spectral characteristics of faecal samples of red deer and concentrations of faecal nitrogen (FN), faecal acid detergent fibre (FADF), and faecal neutral detergent fibre (FNDF).

Constituent	N	R^2	RMSEC	RMSECV	RPD
N	100	0.99	0.03	0.18	2.8
ADF	100	0.98	1.21	4.42	2.9
NDF	100	0.99	0.58	3.55	2.4

Note: N = number of samples used for calibration; R^2 = the degree of correlation between the predicted values and the actual measured values; RMSEC = root mean square error of calibration; RMSECV = root mean square error of cross-validation; RPD = ratio of standard deviation of laboratory reference values and the root mean square error of prediction; RPD ≥ 2 indicates good models.

Concentrations of FN, FADF and FNDF showed the basic values in red deer feaces collected within and outside the overwintering enclosures in individual study areas (Table 3).

Table 3. Concentrations of FN, FADF, and FNDF in red deer faeces. The mean (±SD), minimum, and maximum values of faecal nitrogen (FN), faecal acid detergent fibre (FADF), and faecal neutral detergent fibre (FNDF) in red deer faeces collected from fenced overwintering enclosures and neighbouring unfenced areas within two study areas (MTA Hradiště and MTA Boletice) during winter 2013.

	enclosure				Free-ranging area			
FN	μ±SD	n	Min	Max	μ±SD	n	Min	Max
MTA Hradiště	2.17 ± 0.34	107	1.50	2.88	1.88 ± 0.19	42	1.34	2.28
MTA Boletice	2.21 ± 0.31	79	1.66	3.04	2.27 ± 0.31	82	1.75	3.26
FADF	μ±SD	n	Min	Max	μ±SD	n	Min	Max
MTA Hradiště	44.24 ± 5.13	107	28.10	55.40	47.84 ± 4.22	42	37.10	56.20
MTA Boletice	41.67 ± 4.02	79	33.70	52.30	45.78 ± 3.15	82	36.20	55.00
FNDF	μ±SD	n	Min	Max	μ±SD	n	Min	Max
MTA Hradiště	56.61 ± 5.62	107	38.80	73.80	60.710 ± 3.76	42	52.40	68.00
MTA Boletice	61.48 ± 7.67	79	48.10	75.00	60.80 ± 4.50	82	51.20	71.30

Note: μ – mean, SD – standard deviation; n – number of collected faeces. All values expressed as % dry matter.

The Kendall´s tau τ correlation coefficient showed significant negative relationship between FN and FADF ($\tau_{MTA\ HRADIŠTĚ} = -0.40$, $p < 0.5$; $\tau_{MTA\ BOLETICE} = -0.12$, $p < 0.5$), as well as FNDF ($\tau_{MTA\ HRADIŠTĚ} = -0.65$, $p < 0.5$; $\tau_{MTA\ BOLETICE} = -0.78$, $p < 0.5$) in both study areas. The relationships between FADF and FNDF were positive ($\tau_{MTA\ HRADIŠTĚ} = 0.67$, $p < 0.5$; $\tau_{MTA\ BOLETICE} = 0.16$, $p < 0.5$).

Regarding the differences in individual faecal indices between overwintering enclosure and outside it in the MTA Hradiště, the FN contents were higher in the enclosure compared to the neighbouring area (Wilcox.t.: Z=-4.582; p<0.0001, Fig. 2). The levels of FADF and FNDF showed the opposite trend, with higher levels found in the free-ranging areas compared to the enclosure (ADF: Wilcox. t.: Z=4.040; p<0.0001, Fig. 3; NDF: Student. t-test.: t=4.337; p<0.0001, Fig. 4).

Turning now to the MTA Boletice, the amounts of FN showed a different trend in comparison to MTA Hradiště. The FN levels in the MTA Boletice were similar in the overwintering enclosure and in neighbouring free-ranging area (Wilcox. t.: Z = −0.955; p < 0.3394, Fig. 5). Similarly the concentrations of FADF and FNDF were comparable in the overwintering enclosure and outside it (*ADF*: Wilcox. t.: Z = −0.544; p < 0.5861, Fig. 6; *NDF*: Wilcox. t.: Z = −0.8928; p < 0.3720, Fig. 7).

The amounts of variation in faecal indices of red deer food quality showed interesting patterns in individual study areas. In the MTA Hradiště, the amount of variation was higher in the overwintering enclosure compared to free-ranging area for all studied faecal indices. In the MTA Boletice, on the other hand, the amounts of variation were comparable between the overwintering enclosure and outside it (Table 4).

Table 4. The amounts of variation in faecal indices. Coefficients of variation [%] for faecal indices of food quality for red deer in overwintering enclosures and neighbouring free-ranging areas in MTA Hradiště and MTA Boletice.

	MTA Hradiště		MTA Boletice	
	enclosure	Free-ranging area	enclosure	Free-ranging area
FN	16	10	14	14
FADF	12	9	7	6
FNDF	10	6	8	7

Coefficient of variation (%) was estimated as the ratio of the standard deviation to the mean.

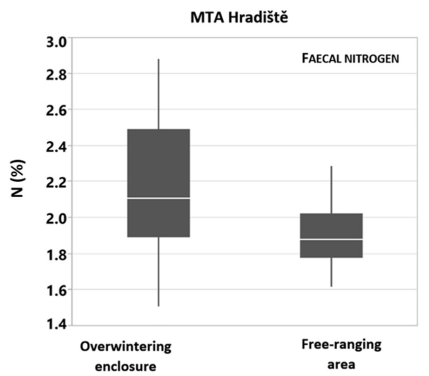

Fig. 2. Volume of nitrogen. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of *faecal nitrogen* in red deer faeces collected in the overwintering fenced enclosures and neighbouring free-ranging areas in the MTA Hradiště.

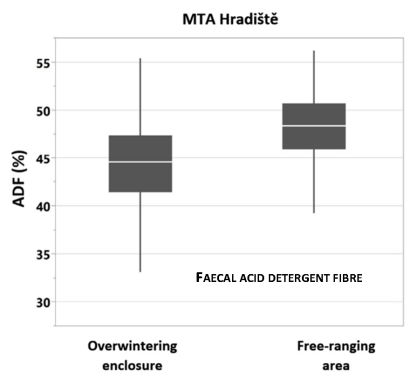

Fig. 3. Volume of ADF. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of *faecal acid detergent fibre* in red deer faeces collected in the overwintering fenced enclosures and neighbouring free-ranging areas in the MTA Hradiště.

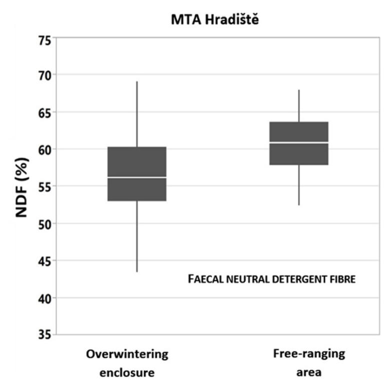

Fig. 4. Volume of NDF. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of *faecal neutral detergent fibre* in red deer faeces collected in the overwintering fenced enclosures and neighbouring free-ranging areas in the MTA Hradiště.

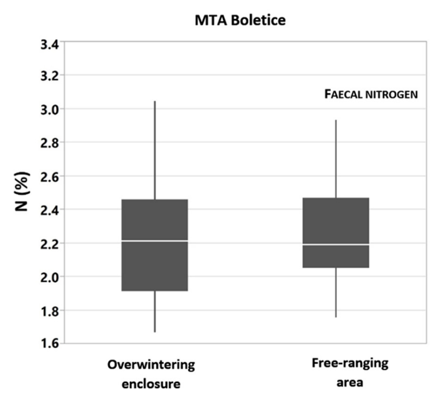

Fig. 5. Volume of nitrogen. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of *faecal nitrogen* in red deer faeces collected in the overwintering fenced enclosures and neighbouring free-ranging areas in the MTA Boletice.

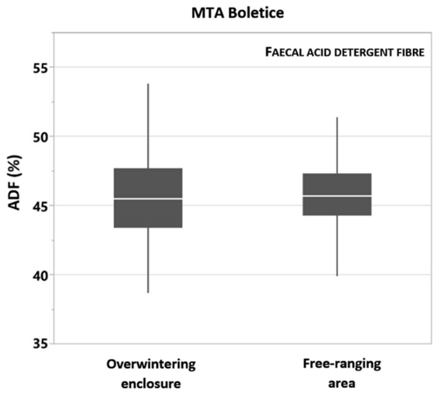

Fig. 6. Volume of ADF. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of *faecal acid detergent fibre* in red deer faeces collected in the overwintering fenced enclosures and neighbouring free-ranging areas in the MTA Boletice.

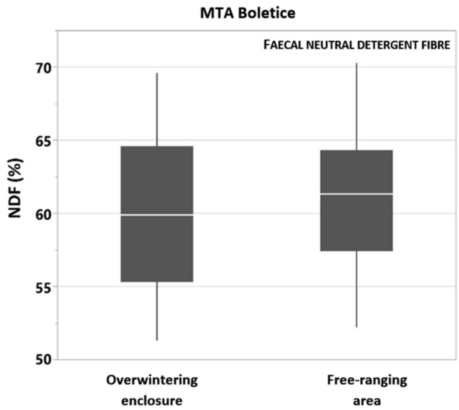

Fig. 7. Volume of NDF. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of *faecal neutral detergent fibre* in red deer faeces collected in the overwintering fenced enclosures and neighbouring free-ranging areas in the MTA Hradiště.

4. Discussion

The use of FN as a proxy for food quality of herbivorous ungulates is based on the fact, that there is a positive relationship between dietary N and FN (e.g. Leslie & Starkey 1985; Hodgman et al. 1996). Nevertheless, it cannot always be assumed that dietary N is directly reflected in the faeces, particularly due to possible effects of secondary metabolites (e.g. Palo & Robbins 1991; Leslie et al. 2008). Therefore, conclusions based only on the FN levels should be strengthened by the use of multiple nutritional indices, such as fibre fractions in faeces (FADF and FNDF). These indices should be more sensitive to fluctuations in food quality than FN, especially when diets contain high amounts of secondary metabolites such as tannins (Hodgman et al. 1996; Leslie et al. 2008). As expected, our results showed a strong negative relationships between FN and FADF, as well as FNDF. This is due to the FN levels being lower if the diet contains more indigestible compounds, such as fibre components, since FN is associated with indigestible fibre (Van Soest 1994).

Our analyses showed that in the MTA Hradiště, the FN concentrations were higher in the overwintering enclosures compared to neighbouring free-ranging areas. The FADF and FNDF levels showed the opposite trends. On the other hand, the food quality indices were similar in the overwintering enclosure and outside it in the MTA Boletice. The observed differences in concentrations of faecal indices at individual study areas are most probably related to animal densities. The density of animals was significantly higher in the overwintering enclosure in the MTA Hradiště (i.e. animal density ranged from 22 to 24 individualsper ha) in comparison to the enclosure in the MTA Boletice, where the animal density was lower (i.e. 4 to 5 individuals per ha). Therefore, at high densities, there may be less plant species of higher quality for red deer as a consequence of over-browsing, thus favouring the growth of woody plant species which are less palatable for red deer (Suzuki et al. 2008). Such plant species have higher concentrations of tannins which are able to bind to plant proteins in the digestive tract of ruminants and thus reduce the levels of digestible protein and increase the excretion of FN (Palo & Robbins 1991; Robbins 1993). This could explain the higher FN values observed in the overwintering enclosure in the MTA Hradiště. Similarly Carpio et al. (2015) have found the highest FN values in areas with the highest red deer densities and tannin concentrations in faeces. On the other hand, other studies focusing on ungulate diets have observed a negative relationship between FN and population density, for example Sams et al. (1998) for white-tailed deer (*Odocoileus virginianus*), and Asada & Ochiai (1999) for sika deer (*Cervus nippon*). These authors have argued that as population density increases, competition for high quality plant species is higher and consequently the high quality plant species are rapidly depleted and the consumed food is of lower quality resulting in decreased FN levels (Sams et al. 1998; Asada & Ochiai 1999).

Another possible explanation for the observed trends in faecal indices in the MTA Hradiště could be the fact that the red deer in the overwintering enclosure were to a larger extent dependent on supplemental foods provided by hunters, which is of better nutritional value and more palatable than winter plant species available outside the enclosure. As reported by Carpio et al. (2015), a positive relationship was found between FN and dietary N in plants on hunting estates with a supplemental food supply, whereas no relationship was observed in the absence of supplementary feeding.

The different degrees of variation in food quality observed in this study may be again attributed to the differences in animal density. Increased population densities may lead to intensified competition for food resources and thus only highly socially ranked individuals are more successful at obtaining foods of high quality (Clutton-Brock & Albon 1985; Putman & Staines 2004). The higher amounts of variation in food quality observed in the enclosure in the MTA Hradiště could hence be attributed to the differential access to high quality foods related to social rank (e.g. Appleby 1980; Thouless 1990). In the MTA Boletice, on the other hand, the amounts of variation were similar in the enclosure and outside it, most probably due to adequate population densities in the area and not intense competition for food resources.

To sum up, the results obtained suggest that the red deer food is of different quality and variability in the overwintering enclosure and neighbouring free-ranging area most probably due to high population density. Therefore, it is necessary to keep animals in overwintering enclosures at moderate densities and to provide high quality forage to all individuals in order to balance nutrition of both the individuals inside and outside the enclosures. Moreover, the analyses confirmed the high potential of NIRS for analysing large numbers of samples necessary for monitoring purposes of red deer diets. However, further studies are needed in order to provide deeper knowledge on red deer food quality and its variability in space and time. The further studies should aim to evaluate the differences in each sex and age classes especially.

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