https://doi.org/10.17221/19/2023-JFS

Are they both the same shit? Winter faeces of roe and red deer show no difference in nutritional components

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Citation: Čupić S., Ježek M., Ceacero F. (2023): Are they both the same shit? Winter faeces of roe and red deer show no difference in nutritional components. J. For. Sci., 69: 114–123.

Abstract: Herbivorous ungulate diets affect population performance and overall forest health through balanced interactions on plant-herbivore relations; therefore, understanding them is critical. Faeces are frequently used in ungulate nutritional ecology because they can provide information about animals' digestive efficiency. Roe deer (*Capreolus capreolus*) and red deer (C*ervus elaphus*) have different morpho-physiological and ecological constraints, and these differences should be reflected in their faeces. On the other hand, the lack of information about the animal (sex, age, reproductive status, diet selection, etc.) may be challenging for such studies. This study aimed to detect species' different susceptibility to these factors reflected in animals' faeces. Thus, we hypothesised that near-infrared reflectance spectrometry (NIRS) could distinguish between the faecal nutrients of two cervids. We collected 94 usable faeces from both species along the forest transect in Bohemian forests in the Czech Republic, covering 2 500 ha. Roe and red deer overlap was determined using the four faecal nutritional components on two axes. No discrimination occurred, refuting our hypothesis and highlighting that out-of-control variables are critical for faecal studies in uncontrolled settings. Fibrous parts explained the most variance (48%), indicating animals' strong reliance on nutrition quality. Apparently, uncontrolled supplementary feeding produced similar faecal nutrient outcomes during the nutrition-limiting winter, which was theoretically supported by the animal's response to predation and hunting pressure. The inability of NIRS to identify the source of N in faeces may also explain the lack of discrimination.

Keywords: *Capreolus capreolus*; *Cervus elaphus*; diet overlap; faecal nutrients; fibre; nitrogen; nutritional ecology

The nutritional quality of the feed ingested determines wild ungulate populations' performance and well-being, which is, at the same time, essential for maintaining healthy forest habitats (Parker et al. 1999, 2009; Christianson, Creel 2007; Felton et al. 2017). Understanding the ungulates' feeding behaviour and the drivers of diet selection regarding nutritional quality, chemical defence, and availability has been of high interest to scientists (Naiman 1988; Hodgman et al. 1996; Barboza et al. 2009; Lambert, Rothman 2015; Corlatti 2020) but is often overlooked during management and conservation decision-making (Morgan et al. 2021). After Raymond (1948) and Lancester (1949) described how the organic matter digestibility of pasture could be calculated from the nitrogen content of the faeces, the use of faecal nitrogen (fN) as a research proxy has been extensively applied in ecological research, and especially in studies related to the nutrition of wild ruminants (Putman 1984; Leslie Jr, Starkey 1987; Osborn, Jenks 1998; Dryden 2003; Leslie Jr et al. 2008). Certainly, there are circumstances in which fN is limited as a nutritional quality indicator for wildlife ungulates in natural settings due to numerous interacting factors that directly or indirectly affect animal nutrition. For instance, high parasite load alters N metabolism and increases fN output (Gálvez-Cerón et al. 2013), or tannins can directly or indirectly affect food intake, digestive efficiency, or protein digestibility through binding to digestive enzymes (Robbins et al. 1987). Furthermore, recent studies have shown that faecal nutritional components can also be influenced by individual factors at the intra-specific level [factors that cannot be controlled for in studies in the wild (Čupić et al. 2021)] and by species-specific differences in digestive capability (Mould, Robbins 1982; Redjadj et al. 2014). Nevertheless, a simultaneous study of other faecal nutritional fractions like lignin (fLig) and acid (fADF) and neutral detergent fibre (fNDF) may help to draw a better picture of the diet quality. Nowadays, this can be achieved through a fast and cheap technique like near-infrared reflectance spectrometry (NIRS) (Putman 1984; Leite, Stuth 1995; Foley et al. 1998; Dryden 2003; Tolleson et al. 2005; Landau et al. 2006; Showers et al. 2006; Gálvez-Cerón et al. 2013; Villamuelas et al. 2017). Indeed, the technique has already been successfully used for estimating the diet quality of roe and red deer in the Czech Republic (Kamler et al. 2004).

These large ungulates are commonly classified along the browser-intermediate-grazer continuum in the context of botanical diet composition (Clauss et al. 2008, 2010; Codron et al. 2019). Roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) are the two most widely distributed cervid species in Europe (Tixier, Duncan 1996; Burbaitė, Csányi 2009, 2010). The roe deer is a small-bodied concentrate selector (browser) that selectively ingests the vegetative parts of herbaceous and woody plants (leaves, buds, and twigs), fruits, and forbs (Hofmann 1988; Tixier, Duncan 1996). As predicted from the digestive morphology and body size of this concentrate selector, they tend to depend on high-quality low-fibre food items (Illius, Gordon 1992) and consume plants with low cell wall contents (Jung, Allen 1995). Grasses usually do not form a large part of the roe deer diet due to the large volume of poorly digestible fibre (Danell et al. 1994). On the contrary, the red deer is classified as an intermediate feeder (generalist). They can adapt to either browsing or grazing, shifting according to plant availability (Hofmann 1989; Langvatn, Hanley 1993). Their general patterns of diet selection focus on maximising the energy intake rate and minimising the intake of antinutritional or toxic compounds (Hanley 1997). Red deer select concentrate food items when the overall browse quality and availability are high (during the vegetation season) and switch to a grass-based diet in response to the decline of concentrate food availability which usually occurs during winter (Dumont et al. 2005; Verheyden-Tixier et al. 2008). In the Bohemian Forest (Central Europe), both deer species display their typical feeding strategies (Barančeková et al. 2010; Krojerová-Prokešová et al. 2010). Meadows are the favourite sites providing a diversity of protein-rich plants significant for the winter diets of both species (Zweifel-Schielly 2005; Hewison et al. 2009; Bonnot et al. 2013), but spruce (*Picea abies*) also constitutes an important portion of their diets (Homolka 1995; Mysterud et al. 1997, 2002; Barančeková et al. 2010; Krojerová-Prokešová et al. 2010). Furthermore, meadows, as a part of the contemporarily frequent fragmented mosaic natural habitats across Europe, are particularly favourable sites for roe deer (Hewison et al. 2001; Jepsen, Topping 2004), which often visit them in search of plants or plant parts that are indispensable for their more selective diet when compared to the one of red deer.

Despite the certain similarities in the winter diets of roe and red deer (Spitzer et al. 2020), partly due to the low food quality and availability, species-specific factors like differences in their digestive tract allow to predict the existence of differences in the faecal nutrients: in fibres due to the different quality of the selected diet, and in nitrogen because of the species-specific digestive efficiency (Hofmann et al. 1988; Hofmann 1989; Clauss, Rössner 2014). Furthermore, distinct life-history traits of these two species should be the source of variety regarding nutritional needs and the capability to fulfil them. Therefore, we hypothesise that the set of overall influencing factors will be clearly reflected in species' faecal samples – roe and red deer will excrete distinguishable faeces in their composition of fN, fADF, fNDF, and fLig. Consequently, we will test the NIRS and provide an insight into its applicability level for wildlife, game, and forest management and whether it can depict these fluctuations that reflect the ungulate-feed interaction and the difference in their morphophysiological-induced differences. The potential differences in faecal nutrients between samples collected in meadows and forests would also be tested (Ossi et al. 2017). However, considering the size-scale of the area in this experiment, its associated mosaic landscape structure, the large home range of these species, and their long food retention time, we did not set our hypothesis based on previous arguments, but rather include this analysis as support to the main research hypothesis.

MATERIAL AND METHODS

The study area is situated in the Bohemian Forest, outside the Šumava National Park in the Czech Republic. This is a forested mountain area and the most continuous mountain range in Central Europe, approximately 130 km long and 60 km wide. Elevation ranges from 370 m a.s.l. to 1 456 m a.s.l., and the climate is continental with a light maritime influence. The mean annual temperature is 6.5 °C in the valleys and 2 °C at higher elevations. Annual precipitation ranges from 400 mm to 2 500 mm without a dry period, but a considerable amount of precipitation occurs as snowfall. Snow cover persists for 7–8 months at higher elevations and 5–6 months in the valleys (this might have undergone certain changes due to the global climate conditions changes in the last years). Cold air pockets are often present in the valley bottoms, leading to an inversion of the thermal gradient, especially in winter. The coldest period is December and January, when temperatures could drop below –15 °C (Heurich et al. 2015).

The area is dominated by Norway spruce (*Picea abies*) with European beech (*Fagus sylvatica*), silver fir (*Abies alba*), and larch (*Larix* sp.). There are some other tree species, such as white birch (*Betula pendula*), sycamore maple (*Acer pseudoplatanus*), and common rowan (*Sorbus aucuparia*) (Wild et al. 2004). We also noticed the presence of aspen (*Salix* sp.) and poplar (*Populus* sp.) in the area. The understorey is dominated by brambles (*Rubus* sp.), which were found to be an important food resource for roe deer (Moser et al. 2006), common honeysuckle (*Lonicera eryclimenum*), ivy (*Hedera helix*) and butcher's broom (*Ruscus aculeatus*). Forest covered most of the study area (Figure 1), while the proportion of meadows was around one-third (Mašková et al. 2009; Voženílková et al. 2010).

The roe and red deer co-occur in the area, 0.6 and 2.9 individuals per km^2, respectively (Košnář, Rajnyšová 2012). Wild boar (*Sus scrofa*) is also widely distributed in the area, while moose (*Alces alces*) is found only in small numbers in the southern part. The main large predator is the Eurasian

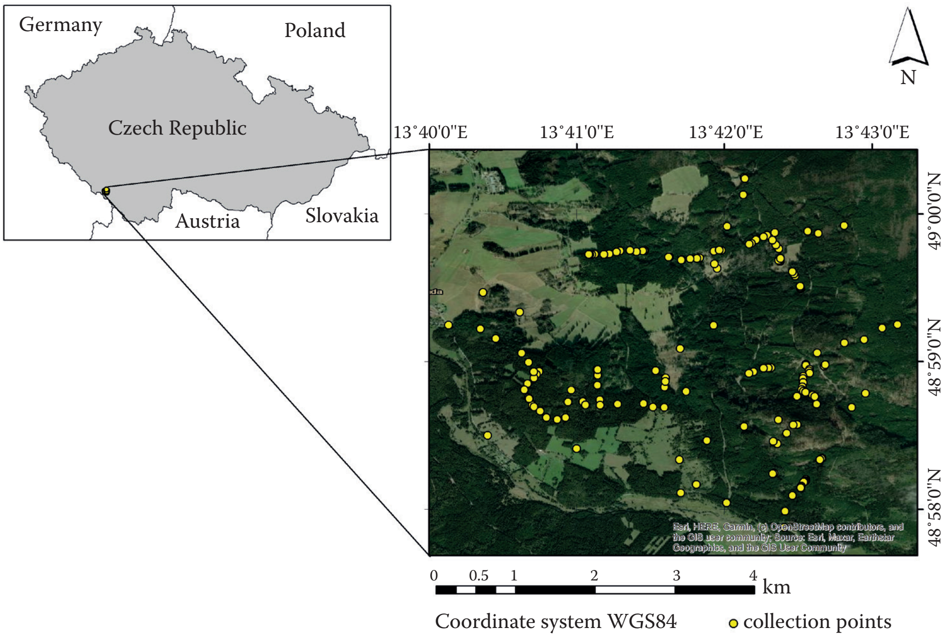

Figure 1. Study area, situated outside the protected zone in the Czech part of Bohemian forests, encompassing approximately 2 500 ha, with meadows comprising around one-third of the area (yellow dots represent sampling spots)

lynx (*Lynx lynx*) which preys mainly on roe deer and, to a much lesser extent, on red deer calves (Heurich et al. 2012). Nevertheless, a wolf appearance has been reported in the area recently (Dvořák 2018; Janík 2020), although that happened after the samples for this study were collected. There is no significant agricultural activity nearby; crop feeding is therefore not common in the area.

We collected 156 faecal pellet groups from roe and red deer along 51.97 km of transects which covered an area of approximately 2 500 ha (Figure 1) at elevations between 782 m a.s.l. and 1 079 m a.s.l. The collection of the samples was conducted in December 2016 and the following January. Snow cover was present during the days of sampling, which facilitated the collection of fresh (recently exposed) faecal samples and avoided soil contamination. Samples in the close surroundings of previously collected samples were discarded to avoid repeated sampling of the same individuals. Discrimination between roe and red deer samples was done by *in situ* visual identification of morphological features (shape and size), further supported by animal tracks in the snow in the approximate vicinity of the sample group. Once in the lab, we calculated the length/width ratio to classify the samples according to their shape [following Chame (2003)] and discarded samples with outlier values (probably calves/fawns). The remaining samples were further confirmed by a senior expert researcher (Prof. Jaroslav Červený). All samples that were unclear to determine or did not pass the previous methodological criteria were discarded. Thus, we finally analysed 94 confirmed samples, 59 for red deer and 35 for roe deer.

The fresh faecal pellet groups were stored in plastic bags and labelled. Afterwards, we air-dried the samples at 50 °C for 48 h, ground them to pass a 1-mm sieve, and mixed them until being homogeneously distributed. We used NIRS^{TM} DS 2500 FOSS analyser under the ISIscan^{TM} Routine Analysis Software (Foss, Denmark) for scanning the samples and obtaining their near-infrared spectra, following Čupić et al. (2021). The contents of *fN*, *fNDF*, *fADF* and *fLig* were calculated with WinISI 4 Calibration Software (Foss, Denmark), according to a calibration set previously developed for red deer faecal samples (Holá et al. 2016) based on 100 samples, which showed a very high predictive power ($R^2 > 0.98$). To increase the robustness of the results, 21 samples with at least one faecal nutrient showing high global and neighbourhood distances (GH1 and NH1) were discarded. Thus, the final dataset consisted of 45 red deer and 28 roe deer samples.

Statistical analyses. The independent samples *t*-test was used to detect differences in faecal nutrients between the studied species and, within each species, between forest and meadow locations. Levene's test for equality of variances was applied in this procedure. Pearson correlations showed the relationships among the four faecal nutrients analysed (*fN*, *fADF*, *fNDF*, *fLig*). Since these were highly correlated, principal component analysis (PCA) was conducted based on these four faecal nutrients to obtain two axes. Varimax rotation with Kaiser normalisation was used as an extraction method to minimise the number of components extracted. Only those components with eigenvalues above 1 were selected. These axes were used to determine the overlap or discrimination between red and roe deer samples and between forest and meadow samples. For the interpretation of the selected axes, only the variables correlating > 0.7 were considered.

RESULTS

The *t*-test analyses failed to detect differences in the winter faecal nutrients between red and roe deer: *fN* (2.54% vs 2.50% respectively for red and roe deer; $t = -0.637$, $P = 0.526$), *fNDF* (56.4% vs. 56.3%; $t = 0.043$, $P = 0.965$), *fADF* (38.3% vs. 38.7%; $t = -0.315$, $P = 0.754$), *fLig* (29.3% vs 30.2%; $t = -1.243$, $P = 0.218$). Similarly, no differences were detected in the winter faecal nutrients of red and roe deer collected in meadow and forest habitats, with just a marginally significant difference in *fN* content in roe deer (2.48% in forest vs. 2.67% in meadow; $t = 1.941$, $P = 0.064$).

The four faecal nutrients analysed were significantly correlated in the 69 samples analysed, ex-

Table 1. Pearson correlations of the studied faecal nutritional components ($N = 94$)

Faecal nutritional components	*fN*	*fADF*	*fNDF*
fADF	-0.368^{**}	–	–
fNDF	-0.658^{***}	0.831^{***}	–
fLig	0.577^{***}	-0.083^{ns}	-0.328^{**}

** $P < 0.01$, $^{***}P < 0.001$; ^{ns}non significant; *fN* – faecal nitrogen; *fADF* – faecal acid detergent fibre; *fNDF* – faecal neutral detergent fibre

https://doi.org/10.17221/19/2023-JFS

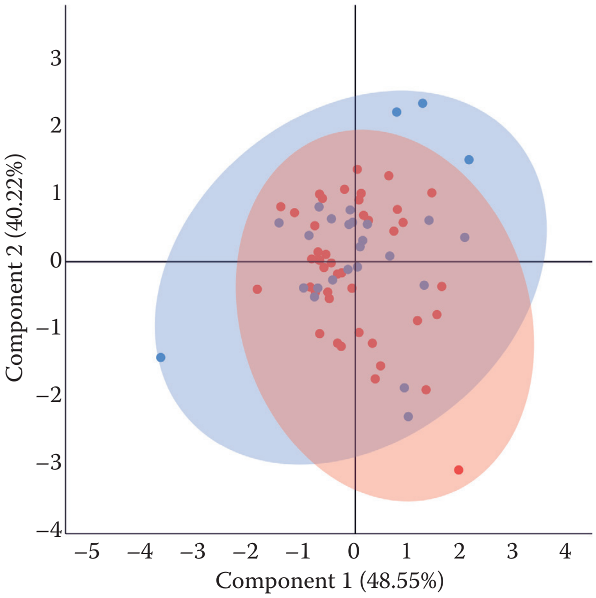

Figure 2. Graphical representation of the samples studied for red deer and roe deer along two axes based on faecal nutrients; component 1 is linked to the fibrous components *fADF* and *fNDF*, while faecal lignin and nitrogen are linked to component 2

Red – red deer; blue – roe deer; *fADF* – faecal acid detergent fibre; *fNDF* – faecal neutral detergent fibre

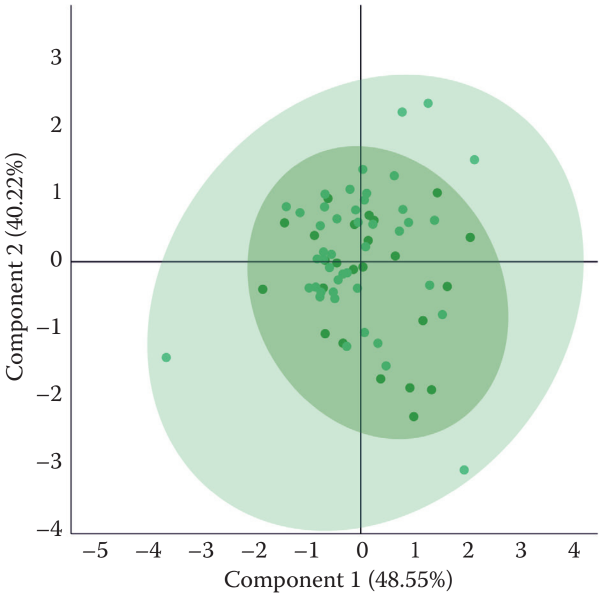

Figure 3. Graphical representation of the samples studied based on the collection habitat along two axes based on faecal nutrients; component 1 is linked to the fibrous components *fADF* and *fNDF*, while faecal lignin and nitrogen are linked to component 2

Dark green – forest; light green – meadows; *fADF* – faecal acid detergent fibre; *fNDF* – faecal neutral detergent fibre

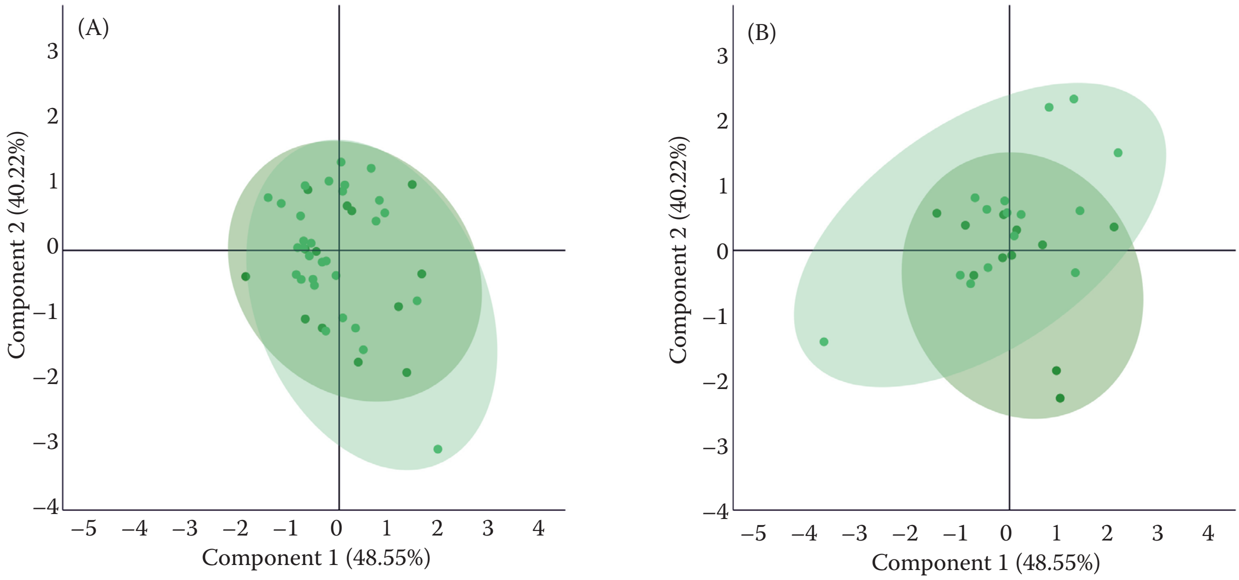

Figure 4. Graphical representation of the samples studied for (A) red deer and (B) roe deer along two axes based on faecal nutrients; component 1 is linked to the fibrous components *fADF* and *fNDF*, while faecal lignin and nitrogen are linked to component 2

Light green – samples collected in meadow habitats; dark green – samples collected in forest habitats; *fADF* – faecal acid detergent fibre; *fNDF* – faecal neutral detergent fibre cept *fLig* and *fADF* (Table 1). The PCA selected two components (axes) with eigenvalues above 1, well representing the original dataset of faecal nutrients. The first component (eigenvalue = 1.942) explained 48.55% of the variance and correlated with *fADF* (r = 0.963) and *fNDF* (r = 0.904). The second component (eigenvalue = 1.609) explained 40.22% of the variance and correlated with *fLig* (r = 0.934) and *fN* (r = 0.781). The plots of the samples studied on these two axes do not allow for discrimination between red and roe deer samples (Figure 2), and neither between samples collected from the forest and meadow habitats (Figure 3). When analysed separately for each species, it was not possible to discriminate between samples from the forest and meadow habitats neither in red (Figure 4A) nor roe deer (Figure 4B).

DISCUSSION

Even under the numerous environmental, species-specific, and animal-specific factors (susceptible to continuous spatiotemporal changes) directly or indirectly connected to the diet selection of red and roe deer, our hypothesis of different winter faecal nutrients between both species was not supported. The four faecal nutritional components grouped in two axes were used for determining the overlap between roe and red deer, but no discrimination was observed. The component that explained the highest portion of variance (48%) correlated with fibrous components, indicating animals' strong reliance on the quality of ingested nutrition.

In this research, the wide variety of environmental, morphophysiological (species-specific), and animal-specific factors and the complexity of their interrelatedness are unknown, which is indeed a general characteristic of most research conducted in natural settings. According to our previous study (Čupić et al. 2021), factors such as pregnancy, pasture availability, and even physical condition or body weight can induce significant variations in faecal output, even when animals consume a similar diet. Thus, under controlled or captive environments, intra- and inter-specific differences in faecal nutrients are indeed observed. However, in nature, where all these factors are unknown, and animals have free access to a greater diversity of plant species, it is extremely improbable that their diet similarity will be even close to that of populations in a controlled environment. Different rations of even the few sources available during the nutritionally-limiting winter season and the attendant specific morphophysiological response during the processes of ingestion, retention, digestion, and excretion should shape their final output. Tannins, already mentioned, could further support this interspecific diet dissociability. Simultaneously, in such a context, it is even more difficult to predict animals' energy expenditure, as well as inter- or intra-specific variation in required energy and, consequently, intraspecific dietary preference. Winter supplementary feeding of large mammalian herbivores is a common management tool in the Czech Republic (Conover 2001; Hothorn, Müller 2010; Möst et al. 2015) and elsewhere, mainly aiming at promoting healthy populations and increasing productivity and trophy sizes. Hunters in our research area provided that, but in low amounts considering the density of cervids. We were unable to obtain exact information either about the amount or about the ratio of supplementary feeding provided since it is a non-protected area. The decision-making process is in the hands of local hunters who do not have strict protocols to follow regarding supplementary feed or a defined law to comply with. Indeed, none of the previous research in this area provided information about this procedure. However, we did not expect a strong impact of supplementary feed, taking into consideration the entire set of previously mentioned potential influencing factors and experience from our previous research with captive animals. Given the almost total overlap observed in the nutritional outputs of both species, predominantly explained by the food quality ingested, the role of the supplementary feed should be further discussed.

The long retention times should be advantageous for ungulate species during harsh winter conditions. Ruminants with higher body mass are prone to having a larger relative gut fill, which leads to increased mean retention time (Demment, Van Soest 1985; Illius, Gordon 1992; Robbins 1993; McNab 2002). Moreover, browsers like roe deer have smaller digestive tracts and shorter retention times than grazers or intermediate feeders [three times larger rumen as a percentage of body weight in red deer compared to roe deer (Prins, Geelen 1971)]. Higher tolerance to fibrous forage has also been attributed to the same interspecific differences (Hofmann, Stewart 1972; Hofmann 1989; Clauss, Lechner-Doll 2001; Clauss et al. 2003). In habitats where ungulates must account for expensive activities such as avoiding hunting and predation, this benefit is increased as energy expenditures are higher. The maintenance requirements may increase with movement and stress by as much as 200–300% (Weiner 1977). Therefore, large ungulates often find themselves in a trade-off between shelter and food search. According to this, that trade-off should be easier to solve by red deer compared to roe deer, given its body size and previously discussed morpho-physiological characteristics. In a scenario where animals must rely exclusively on natural feed sources, roe deer acts as a typical browser, selecting diets with a higher nutritional value in terms of high protein content and avoiding high-fibre diets (Drescher-Kaden, Seifelnasr 1977; Hofmann 1989; Duncan et al. 1998). Given the morpho-physiology of the species, in times of increased energy demands (e.g. heat production during winter), this means reduced locomotor activity and higher exposure to hunting and predation. However, when increased amounts of carbohydrates are available in the form of supplementary feed, these may be mainly consumed by roe deer since that may be of higher vital importance for them than for red deer. The supplementary feed may thus help both species, but especially roe deer, to survive the winter while feeding on natural plant species with low nutritional value (Miranda et al. 2015), leading to more similar diets than initially expected and thus to similar faecal nutrients.

The above explanations can be supported by further incorporating the impact of predators and hunting pressure on the distribution, habitat preference, and nutritional ecology of roe and red deer in the study area. The Eurasian lynx (*Lynx lynx*) is the main predator in the area, predominantly preying on roe deer but also on young red deer individuals. As already commented, hunting pressure is relatively high in the area for both species, with greater exploitation of red deer due to their attractive trophies. That may induce stress in both species, and the consequence may be lower time searching for food, lower feed quality and increased compensation through the supplementary feed. In the study area, supplementary feeders are usually situated on the edges of forests and meadows, the habitat preferred by roe deer (Heurich et al. 2015). Indeed, this same study showed that roe deer in Bohemian forests prefer unprotected areas, despite the high impact of hunting, over protected areas of the park due to the supplementary feeding provided by hunters out of the national park. In contrast, red deer prefer vegetation-dense forest habitats of around 70% of cover (Heurich et al. 2015). In these areas, the shrub vegetation layer, which red deer can use, stands during winter. Red deer probably keep feeding on this resource more extensively than roe deer due to the necessity to reach a certain threshold of fibres for supporting the proper functioning of their large rumens (Bauchop 1979; Gebert, Verheyden-Tixier 2001), thus showing less dependence on supplementary feed.

CONCLUSION

The inability of NIRS to identify the source of N in faeces may be another reason behind the lack of discrimination between free-ranging roe and red deer faecal samples. The difficult interpretation of *fN* has been mentioned in previous research (Čupić et al. 2021). This problem might be solved in future studies by analysing the amount of N bound to ADF (Van Soest 2018), which would allow the calculation of metabolic faecal nitrogen (MFN). That would inform about the proportion of N being used by the animal cell function and not only excreted by it. Such analysis would confirm if there was an actual lack of differences in the diet consumed by both species or if our hypothesis was rejected just because of the inability of NIRS to detect the source of protein excreted. Even if the second reason was correct, certain discrimination at the axis explained by fibres could still have been found.

Altogether, the results thus suggest that NIRS and the analysis of faecal nutrients should not be employed for this type of research during periods when dietary overlaps across species can be expected, but especially when we have neither other sources of information about what the animals could have consumed (e.g. camera traps, direct observation, or GPS collars), nor information about each individual. The sum of uncontrolled factors may easily lead to non-significant results, which, theoretically, should have been expected. That may subsequently lead to making incorrect management decisions.

REFERENCES

Barančeková M., Krojerová-Prokešová J., Šustr P., Heurich M. (2010): Annual changes in roe deer (*Capreolus capreolus* L.) diet in the Bohemian Forest, Czech Republic/Germany. European Journal of Wildlife Research, 56: 327–333.

Barboza P.S., Parker K.L., Hume I.D. (2009): Integrative Wildlife Nutrition. Berlin, Heidelberg, Springer: 342.

Bauchop T. (1979): The rumen anaerobic fungi: Colonisers of plant fibre. Annales De Recherches Veterinaires, 10: 246–248.

Bonnot N., Morellet N., Verheyden H., Cargnelutti B., Lourtet B., Klein F., Hewison A.M. (2013): Habitat use under predation risk: Hunting, roads and human dwellings influence the spatial behaviour of roe deer. European Journal of Wildlife Research, 59: 185–193.

Burbaiteė L., Csányi S. (2009): Roe deer population and harvest changes in Europe. Estonian Journal of Ecology, 58: 169–180.

Burbaitė L., Csányi S. (2010): Red deer population and harvest changes in Europe. Acta Zoologica Lituanica, 20: 179–188.

Chame M. (2003): Terrestrial mammal feces: A morphometric summary and description. Memórias do Instituto Oswaldo Cruz, 98: 71–94.

Christianson D.A., Creel S. (2007): A review of environmental factors affecting elk winter diets. The Journal of Wildlife Management, 71: 164–176

Clauss M., Lechner-Doll M. (2001): Differences in selective reticulo-ruminal particle retention as a key factor in ruminant diversification. Oecologia, 129: 321–327.

Clauss M., Rössner G.E. (2014): Old world ruminant morphophysiology, life history, and fossil record: Exploring key innovations of a diversification sequence. Annales Zoologici Fennici, 51: 80–94.

Clauss M., Frey R., Kiefer B., Lechner-Doll M., Loehlein W., Polster C., Rössner G.E., Streich W.J. (2003): The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. Oecologia, 136: 14–27.

Clauss M., Kaiser T., Hummel J. (2008): The morphophysiological adaptations of browsing and grazing mammals. In: Gordon I.J., Prins H.H.T. (eds): The Ecology of Browsing and Grazing. Berlin, Heidelberg, Springer: 47–88.

Clauss M., Hume I.D., Hummel J. (2010): Evolutionary adaptations of ruminants and their potential relevance for modern production systems. Animal, 4: 979–992.

Codron D., Hofmann R.R., Clauss M. (2019): Morphological and physiological adaptations for browsing and grazing. In: Gordon I.J., Prins H.H.T.: The Ecology of Browsing and Grazing II. Cham, Springer: 81–125.

Conover M.R. (2001): Effect of hunting and trapping on wildlife damage. Wildlife Society Bulletin, 29: 521–532.

Corlatti L. (2020): Anonymous fecal sampling and NIRS studies of diet quality: Problem or opportunity? Ecology and Evolution, 10: 6089–6096.

Čupić S., García A.J., Holá M., Ceacero F. (2021): Evaluation of factors inducing variability of faecal nutrients in captive red deer under variable demands. Scientific Reports, 11: 2394.

Danell K., Mikael Utsi P., Thomas Palo R., Eriksson O. (1994): Food plant selection by reindeer during winter in relation to plant quality. Ecography, 17: 153–158.

Demment M.W., Van Soest P.J. (1985): A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. The American Naturalist, 125: 641–672.

Drescher-Kaden U., Seifelnasr E.A. (1977): Tests on the digestive system of roe deer, fallow deer and mouflon, 2: Crude nutritve substances in the rumen content of roe deer, fallow deer and mouflon. Zeitschrift fuer Jagdwissenschaft, 23: 6–11. (in German)

Dryden G.M. (2003): Near Infrared Spectroscopy: Applications in Deer Nutrition. Kingston, Rural Industries Research and Development Corporation: 46.

Dumont A., Ouellet J.P., Crête M., Huot J. (2005): Winter foraging strategy of white-tailed deer at the northern limit of its range. Ecoscience, 12: 476–484.

Duncan A.J., Hartley S.E., Iason G.R. (1998): The effect of previous browsing damage on the morphology and chemical composition of Sitka spruce (*Picea sitchensis*) saplings and on their subsequent susceptibility to browsing by red deer (*Cervus elaphus*). Forest Ecology and Management, 103: 57–67.

Dvořák J. (2018): Správa Národního parku Šumava stanovuje nové území bez lovu a pracuje na nové koncepci přezimovacích obůrek. Available at: https://www.npsumava.cz/sprava-narodniho-parku-sumava-stanovuje-nove-uzemi-bez-lovu-a-pracuje-na-nove-koncepci-prezimovacich-oburek/ (Accessed May 16, 2020; in Czech).

Felton A.M., Felton A., Cromsigt J.P., Edenius L., Malmsten J., Wam H.K. (2017): Interactions between ungulates, forests, and supplementary feeding: The role of nutritional balancing in determining outcomes. Mammal Research, 62: 1–7.

Foley W.J., McIlwee A., Lawler I., Aragones L., Woolnough A.P., Berding N. (1998): Ecological applications of near infrared reflectance spectroscopy – a tool for rapid, cost-effective prediction of the composition of plant and animal tissues and aspects of animal performance. Oecologia, 116: 293–305.

Gálvez-Cerón A., Serrano E., Bartolomé J., Mentaberre G., Fernández-Aguilar X., Fernández-Sirera L., Navarro-González N., Gassó D., López-Olvera J.R., Lavín S., Marco I., Albanell E. (2013): Predicting seasonal and spatial variations in diet quality of Pyrenean chamois (*Rupicapra pyrenaica pyrenaica*) using near infrared reflectance spectroscopy. European Journal of Wildlife Research, 59: 115–121.

Gebert C., Verheyden-Tixier H. (2001): Variations of diet composition of red deer (*Cervus elaphus* L.) in Europe. Mammal Review, 31: 189–201.

Hanley T.A. (1997): A nutritional view of understanding and complexity in the problem of diet selection by deer (*Cervidae*). Oikos, 79: 209–218.

Heurich M.., Möst L., Schauberger G., Reulen H., Sustr P., Hothorn T. (2012): Survival and causes of death of European roe deer before and after Eurasian lynx reintroduction in the Bavarian Forest National Park. European Journal of Wildlife Research, 58: 567–578.

Heurich M., Brand T.T., Kaandorp M.Y., Šustr P., Müller J., Reineking B. (2015): Country, cover or protection: What shapes the distribution of red deer and roe deer in the Bohemian Forest Ecosystem? PLOS One, 10: e0120960.

Hewison A.J., Vincent J.P., Joachim J., Angibault J.M., Cargnelutti B., Cibien C. (2001): The effects of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. Canadian Journal of Zoology, 79: 679–689.

Hewison A.J.M., Morellet N., Verheyden H., Daufresne T., Angibault J.M., Cargnelutti B., Merlet J., Picot D., Rames J.L., Joachim J., Lourtet B., Serrano E., Bideau E., Cebe N. (2009): Landscape fragmentation influences winter body mass of roe deer. Ecography, 32: 1062–1070.

Hodgman T.P., Davitt B.B., Nelson J.R. (1996): Monitoring mule deer diet quality and intake with fecal indices. Rangeland Ecology and Managementt / Journal of Range Management Archives, 49: 215–222.

Hofmann R.R. (1989): Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. Oecologia, 78: 443–457.

Hofmann R.R., Stewart D.R.M. (1972): Grazer or browser: A classification based on the stomach-structure and feeding habits of East African ruminants. Mammalia, 36: 226–240.

Hofmann R.R., Saber A.S., Pielowski Z., Fruziński B. (1988): Comparative morphological investigations of forest and field ecotypes of roe deer in Poland. Acta Theriologica, 33: 103–114.

Holá M., Ježek M., Kušta T., Červený J. (2016): Evaluation of winter food quality and its variability for red deer in forest environment: overwintering enclosures vs. free-ranging areas. Forestry Journal, 62: 139–145.

Homolka M. (1995): The diet of *Cervus elaphus* and *Capreolus capreolus* in deforested areas of the Moravskoslezske Beskydy Mts [Czech Republic]. Folia Zoologica (Czech Republic), 44: 227–236.

Hothorn T., Müller J. (2010): Large-scale reduction of ungulate browsing by managed sport hunting. Forest Ecology and Management, 260: 1416–1423.

Illius A.W., Gordon I.J. (1992): Modelling the nutritional ecology of ungulate herbivores: Evolution of body size and competitive interactions. Oecologia, 89: 428–434.

Janík T. (2020): Bavarian Forest and Šumava National Parks: On the way to transboundary wildlife management and conservation? Silva Gabreta, 26: 51–63.

Jepsen J.U., Topping C.J. (2004): Modelling roe deer (*Capreolus capreolus*) in a gradient of forest fragmentation: Behavioural plasticity and choice of cover. Canadian Journal of Zoology, 82: 1528–1541.

Jung H.G., Allen M.S. (1995): Characteristics of plant cell walls affecting intake and digestibility of forages by ruminants. Journal of Animal Science, 73: 2774–2790.

Kamler J., Homolka M., Čižmár D. (2004): Suitability of NIRS analysis for estimating diet quality of free-living red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. Wildlife Biology, 10: 235–240.

Košnář A., Rajnyšová R. (2012): Determine of population density of red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in the mountain areas of Šumava. Sborník Jihočeského Muzea v Českých Budějovicích, Přírodní Vědy, 52: 221–231. (in Czech)

Krojerová-Prokešová J., Barančeková M., Šustr P., Heurich M. (2010): Feeding patterns of red deer *Cervus elaphus* along an altitudinal gradient in the Bohemian Forest: Effect of habitat and season. Wildlife Biology, 16: 173–184.

Lambert J.E., Rothman J.M. (2015): Fallback foods, optimal diets, and nutritional targets: Primate responses to varying food availability and quality. Annual Review of Anthropology, 44: 493–512.

Lancaster R.J. (1949): Estimation of digestibility of grazed pasture from faeces nitrogen. Nature, 163: 330–331.

Landau S., Glasser T., Dvash L. (2006): Monitoring nutrition in small ruminants with the aid of near infrared reflectance spectroscopy (NIRS) technology: A review. Small Ruminant Research, 61: 1–11.

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

Leite E.R., Stuth J.W. (1995): Fecal NIRS equations to assess diet quality of free-ranging goats. Small Ruminant Research, 15: 223–230.

Leslie Jr D.M., Starkey E.E. (1987): Fecal indices to dietary quality: A reply. The Journal of Wildlife Management, 51: 321–325.

Leslie Jr D.M., Bowyer R.T., Jenks J.A. (2008): Facts from feces: Nitrogen still measures up as a nutritional index for mammalian herbivores. The Journal of Wildlife Management, 72: 1420–1433.

Mašková Z., Doležal J., Květ J., Zemek F. (2009): Long-term functioning of a species-rich mountain meadow under different management regimes. Agriculture, Ecosystems & Environment, 132: 192–202.

McNab B.K. (2002): The Physiological Ecology of Vertebrates: A View from Energetics. Ithaca, Cornell University Press: 576.

Miranda M., Cristóbal I., Díaz L., Sicilia M., Molina-Alcaide E., Bartolomé J., Fierro Y., Cassinello J. (2015): Ecological effects of game management: Does supplemental feeding affect herbivory pressure on native vegetation? Wildlife Research, 42: 353–361.

https://doi.org/10.17221/19/2023-JFS

Morgan L.R., Marsh K.J., Tolleson D.R., Youngentob K.N. (2021): The application of NIRS to determine animal physiological traits for wildlife management and conservation. Remote Sensing, 13: 3699.

Moser B., Schütz M., Hindenlang K.E. (2006): Importance of alternative food resources for browsing by roe deer on deciduous trees: the role of food availability and species quality. Forest Ecology and Management, 226: 248–255.

Möst L., Hothorn T., Müller J., Heurich M. (2015): Creating a landscape of management: Unintended effects on the variation of browsing pressure in a national park. Forest Ecology and Management, 338: 46–56.

Mould E.D., Robbins C.T. (1982): Digestive capabilities in elk compared to white-tailed deer. The Journal of Wildlife Management, 46: 22–29.

Mysterud A., Bjørnsen B.H., Østbye E. (1997): Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* along an altitudinal gradient in south-central Norway. Wildlife Biology, 3: 27–33.

Mysterud A., Langvatn R., Yoccoz N.G., Stenseth N.C. (2002): Large-scale habitat variability, delayed density effects and red deer populations in Norway. Journal of Animal Ecology, 71: 569–580.

Naiman R.J. (1988): Animal influences on ecosystem dynamics. BioScience, 38: 750–752.

Osborn R.G., Jenks J.A. (1998): Assessing dietary quality of white-tailed deer using fecal indices: Effects of supplemental feeding and area. Journal of Mammalogy, 79: 437–447.

Ossi F., Gaillard J.M., Hebblewhite M., Morellet N., Ranc N., Sandfort R., Kroeschel M., Kjellander P., Mysterud A., Linnell J.D.C., Heurich M., Soennichsen L., Sustr P., Berger A., Rocca M., Urbano F., Cagnacci F. (2017): Plastic response by a small cervid to supplemental feeding in winter across a wide environmental gradient. Ecosphere, 8: e01629.

Parker K.L., Gillingham M.P., Hanley T.A., Robbins C.T. (1999): Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. Wildlife Monographs, 143: 3–48.

Parker K.L., Barboza P.S., Gillingham M.P. (2009): Nutrition integrates environmental responses of ungulates. Functional Ecology, 23: 57–69.

Prins R.A., Geelen M.J.H. (1971): Rumen characteristics of red deer, fallow deer, and roe deer. The Journal of Wildlife Management, 35: 673–680.

Putman R.J. (1984): Facts from faeces. Mammal Review, 14: 79–97.

Raymond W.F. (1948): Evaluation of herbage for grazing. Nature, 161: 937–938.

Redjadj C., Darmon G., Maillard D., Chevrier T., Bastianelli D., Verheyden H., Loison A., Saïd S. (2014): Intra- and interspecific differences in diet quality and composition in a large herbivore community. PloS ONE, 9: e84756.

Robbins C.T. (1993): Wildlife Feeding and Nutrition. San Diego, Academic Press: 352.

Robbins C.T., Mole S., Hagerman A.E., Hanley T.A. (1987): Role of tannins in defending plants against ruminants: Reduction in dry matter digestion? Ecology, 68: 1606–1615.

Showers S.E., Tolleson D.R., Stuth J.W., Kroll J.C., Koerth B.H. (2006): Predicting diet quality of white-tailed deer via NIRS fecal profiling. Rangeland Ecology and Management, 59: 300–307.

Spitzer R., Felton A., Landman M., Singh N.J., Widemo F., Cromsigt J.P. (2020): Fifty years of European ungulate dietary studies: A synthesis. Oikos, 129: 1668–1680.

Tixier H., Duncan P. (1996): Are European roe deer browsers? A review of variations in the composition of their diets. Revue d'Ecologie, Terre et Vie, 51: 3–17.

Tolleson D.R., Randel R.D., Stuth J.W., Neuendorff D.A. (2005): Determination of sex and species in red and fallow deer by near infrared reflectance spectroscopy of the faeces. Small Ruminant Research, 57: 141–150.

Van Soest P.J. (2018): 1. Ruminants in the world. In: Van Soest P.J.: Nutritional Ecology of the Ruminant. Ithaca, Cornell University Press: 1–6.

Verheyden-Tixier H., Renaud P.C., Morellet N., Jamot J., Besle J.M., Dumont B. (2008): Selection for nutrients by red deer hinds feeding on a mixed forest edge. Oecologia, 156: 715–726.

Villamuelas M., Serrano E., Espunyes J., Fernández N., López-Olvera J.R., Garel M., Santos J., Parra-Aguado M.**Á**., Ramanzin M., Fernández-Aguilar X., Colom-Cadena A. (2017): Predicting herbivore faecal nitrogen using a multi-species near-infrared reflectance spectroscopy calibration. PLOS One, 12: e0176635.

Voženílková B., Klimeš F., Kobes M., Suchý K., Květ J. (2010): Influence of mowing on phytopathological aspects of mountain meadows dynamics. Ekológia, 29: 290–293.

Weiner J. (1977): Energy metabolism of the roe deer. Acta Theriologica, 22: 3–24.

Wild J., Neuhäuslová Z., Sofron J. (2004): Changes of plant species composition in the Šumava spruce forests, SW Bohemia, since the 1970s. Forest Ecology and Management, 187: 117–132.

Zweifel-Schielly B. (2005): Spatial and nutritional ecology of GPS-collared red deer in an Alpine region: The role of forage availability and quality. [Ph.D. Thesis.] Zurich, Swiss Federal Institute of Technology Zurich.

Received: February 17, 2023
Accepted: March 3, 2023