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ORIGINAL PAPER

# Nutritional niche separation between native roe deer and the nonnative fallow deer—a test of interspecific competition

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## Abstract

On an evolutionary time scale, competition for food drives species formation by genetic adaptations to the environment and subsequent niche separation. On a short-term scale, animals use different strategies to meet their nutritional requirements, which ultimately influence their fitness. Understanding these adaptations in herbivores is especially important in temperate climates where animals have adapted both physiologically and behaviorally to seasonal variations in order to meet their nutritional requirements. The aim of this project was to investigate temporal variation in chemical composition of rumen content between two coexisting species of large herbivores, the native roe deer (*Capreolus capreolus L.*) and the introduced fallow deer (*Dama dama L.*), as well as a potential effect of competition on niche separation (interspecific differences in rumen nutrient composition). We analyzed 345 rumen samples collected from animals at one 95 km$^2$ estate, Koberg, in southwestern Sweden. Based on samples from all seasons, temporal variation in nutrient composition and interspecific differences between the two deer species were investigated under two contrasting fallow deer population densities. Results revealed that nutrient composition varied between species and across seasons. Roe deer had a higher proportion of rumen protein compared to fallow deer, with the highest proportions in spring. In contrast, fallow deer had a higher proportion of rumen hemicellulose compared to roe deer in spring, while no differences in nutrient composition between species could be found in fall. Overall, there were greater differences between the two species when fallow deer density was high and competition likely more pronounced than when fallow deer density was low. The results from this study can be used to understand interspecific competition and how it fosters niche separation between coexisting large herbivores.

**Keywords** Cervidae · Niche separation · Nutritional ecology · Rumen contents

## Introduction

On an evolutionary time scale, competition for food drives species formation by genetic adaptations to the environment (Raubenheimer et al. 2012) and subsequent niche separation of the species (Hardin 1960; Schoener 1974; Codron and Clauss 2010). On a short-term scale, an overlap in habitat use and diet preferences, together with limited food availability, may increase interspecific competition (Putman 1996; Pan et al. 2019; Regmi et al. 2020). In addition, interspecific competition may also increase due to seasonal changes or when population densities increase (Nicholson et al. 2006; Obidziński et al. 2013), and this in turn can increase either overlap or niche separation between competing species depending on e.g., resource availability and environmental conditions (Pianka 1974; Schoener 1974; Araujo et al. 2011; Redjadj et al. 2014). In ungulates, competition is the most commonly described interspecific interaction (Putman 1996). If several species interact by exploitive interactions, it is likely to influence the way in which each species use the common resources. As long as resources are not short in supply, niche segregation may contribute to coexistence to reduce competition at higher

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population densities (Hardin 1960; Pianka 1974; Schoener 1974; Redjadj et al. 2014). However, as food resources becomes limited, sympatric species can be expected to demonstrate niche overlap and competitive interactions (Schoener 1974; Putman 1996; Regmi et al. 2020). Among large herbivore species, browsers are often observed to feed selectively on the most digestible plant materials when available, such as leaves, seedlings, and forbs (Cederlund et al. 1980; Tixier et al. 1997), while grazers are less discriminate feeders of large food quantities and are expected to maintain on abundant but less digestible material. Such differences in feeding strategies have been explained in terms of both physiomorphological adaptations (Hofmann 1989; Clauss et al. 2008; Codron et al. 2019) and as a consequence of body size (Illius and Gordon 1987).

In Northern-Central Europe, as a nonnative species, the fallow deer (*Dama dama L.*) is expected to have a wider resource overlap with the sympatric native cervid species (family Cervidae) in areas where it is introduced than is observed among the native cervids in the same area (Clutton-Brock and Albon 1989; Hemami et al. 2004; Whitney et al. 2011). This is theoretically interesting, in the context of cooccurrence with native species, as it is expected to result in strong patterns of habitat and/or dietary separation as is observed by Svärdson (1976) in native Scandinavian freshwater brown trout (*Salomo trutta L.*) when living in sympatry after introduction of the competing arctic char (*Salvelinus alpinus L.*). Roe deer (*Capreolus capreolus L.*) and fallow deer often share the same general habitats, and in the temperate part of the world, both species are forced to adapt to seasonal variations (Cederlund and Nystrom 1981; Holand 1994; Apollonio and Di Vittorio 2004; Obidziński et al. 2013; König et al. 2020). However, there are reasons to believe that these two species regulate their nutrient intake differently. One reason is their body size. Roe deer having a live weight of 18–31 kg (Liberg and Wahlström 1995; Pettorelli et al. 2002) and show a low level of dimorphism (Carranza 1996), whereas fallow deer is highly sexually dimorphic with a live weight ranging from 39 kg for adult females to 117 kg for males (Carranza 1996; Loison et al. 1999; McElligott et al. 2001). Furthermore, in Northern Europe, the endemic roe deer and the introduced invasive fallow deer represent two very different cases within the Cervidae family. Roe deer are classified as browsers and are adapted to early successional habitats offering relatively nutritious resources (Hofmann 1989; Andersen et al. 1998), whereas fallow deer evolved to more efficiently digest plant cell walls (e.g., cellulose) and are therefore assumed to be able to handle more variable nutritional intakes than roe deer (Hofmann 1989). The most obvious and expected consequence of introducing an exotic species into an area will be one or several of the native species responding negatively (Svärdson 1976). This prediction is interesting in view of public opinion and particularly among Swedish hunters and managers in areas where fallow deer has established (Carlström and Nyman 2005). In such areas it is claimed that fallow deer some years after establishment out-compete, oust, or at least depress roe deer densities and possibly other deer species, too (Carlström and Nyman 2005). This suggests that the smaller and more specialized roe deer suffers severely from direct effects of either exploitive and/or interference competition when confronted with the introduced fallow deer. To our knowledge, such a phenomenon has rarely been demonstrated among deer species in temperate areas (but see Putman 1996, Latham 1999, Ferretti and Mori 2020 for reviews).

In addition to the challenges posed upon these animals in terms of competition and spatial resource distribution, at northern latitudes, forage availability and quality change dramatically between seasons (Van Soest 1994; Marshal et al. 2005). Accordingly, herbivores show behavioral and physiological adaptations to seasons, for example in voluntary feed intake, metabolic rate, body growth, and plasma hormone concentrations (Domingue et al. 1991; Freudenberger et al. 1994; Arnold et al. 2004). Seasonal changes in the availability of food may also influence levels of competition (Storms et al. 2008; Obidziński et al. 2013), which may be further aggravated through increased population densities (Araujo et al. 2011; Obidziński et al. 2013). Fallow deer are adapted to tolerate high population densities (Carlström and Nyman 2005) and increased fallow deer densities (FDD) may therefore mainly increase the competitive pressure on roe deer when these species coexist (Focardi et al. 2006, Ferretti et al. 2008, 2011, Elofsson et al. 2017—from the same study area as this). The fallow deer was introduced to the Nordic fauna for the first time in the Mid-16th century (Chapman and Chapman 1980), but has increased dramatically both in numbers and distributional range mostly in the last 25 years, with a recorded harvest in 2019 of > 55,000 individuals in Sweden (Viltdata 2019). A current estimation of the nutritional composition of ingested food at different seasons and population densities will therefore increase our understanding of the interspecific competition between roe deer and fallow deer, and the associated niche separation or overlap.

In this study, covering several years and all seasons, we analyze the proportions of six nutrient constituents in rumen content as a proxy of the nutritional composition of forage mixtures eaten by coexisting roe deer and fallow deer occurring at contrasting population densities in the same area. We make the assumption that the nutritional composition of rumen content, in particular the relative proportions of digestible fiber (hemicellulose and cellulose) and lignin, roughly mirrors the nutritional composition of ingested forage, acknowledging that digestive processes have changed the composition to a varying extent in sampled individuals (Van Soest 1994).

We predict that (1) both roe deer and fallow deer show seasonal variation in nutrient composition of ingested forage, with more easily digestible forage (relatively high in nonstructural carbohydrates but low in digestible fiber and lignin) ingested in spring and summer compared to fall and winter because of the seasonal differences in availability of easily digestible forage (Van Soest 1994; Marshal et al. 2005). In addition, we predict that (2) roe deer ingest forage higher in protein and nonstructural carbohydrates and lower in digestible fibers compared to fallow deer based on where these two ruminant species are placed on the continuum from browsers to grazers (Hofmann 1989), which is supported by findings by Spitzer et al. (2020) and from the study area by Nichols et al. (2016) who clearly show that fallow deer select grass to a much higher extent than roe deer. Grasses often contain higher concentrations of digestible fiber (both hemicellulose and cellulose) than herbs and browse (Hummel et al. 2006; Verheyden-Tixier et al. 2008). Finally, we predict that (3) the degree of nutritional niche separation between the two deer species will be greater under conditions of relatively high population densities of fallow deer than under low densities, to minimize the effects of interspecific competition, under the assumption that resources are not too limited (e.g., Pianka 1974; Schoener 1974; Putman 1996; Focardi et al. 2006).

## Material and methods

The study was based on 499 rumen samples collected by the project in collaboration with the land owner and hunters on the Koberg estate situated in the southwestern part of Sweden (58°N, 12°E) in Västra Götaland County. The Koberg estate comprises 95 $km^2$ of which the study area covers 81 $km^2$. Furthermore, the study area was divided in 2005 into two management areas where the northern (27 $km^2$) and southern parts (54 $km^2$) are separated by a wildlife-fenced road acting as a barrier and thus limiting animal movements between the two subpopulations. Ungulate densities were estimated by distance sampling (Buckland et al. 2001). Through conscious and planned removal, fallow deer density declined from 19.6 to 7.0 individuals $km^{-2}$ between 2007 and 2008 and thereafter stabilized at 9 individuals $km^{-2}$ in the northern area while it remained high and varied between 22.8 and 39.5 individuals $km^{-2}$ in the southern area from 2007 to 2013, whereas roe deer density varied between 0.1 and 2.8 individuals $km^{-2}$ in the northern area and between 0.2 and 1.8 individuals $km^{-2}$ in the southern area during the study (Kjellander unpublished data). The habitat composition and productivity did not differ between the two subareas and were managed by standard commercial forestry and agricultural practices by the landowner. The two subareas are dominated by forest (80%) of which 50% consist of mature coniferous forest, 20% of clear-felled areas and younger forest, and 10% of mixed- and broadleaved forest (Winsa 2008). The remainder of the habitat is represented by arable land and pastures (15%), lakes, ponds, parks, and properties (3%), as well as mires and marshes (2%) (Winsa 2008; Kjellander et al. 2012). Supplementary feeding is provided regularly by the estate from the 1st of November to the 30th of April, but may vary across years depending on availability of natural forage and/or snow cover (Garrido et al. 2014). The amount and type of food varies among feeding sites, but silage is available for the animals during the whole supplementary feeding period and on most feeding sites, whereas sugar beets, carrots, potatoes, oat etc. are provided occasionally (Garrido et al. 2014). In addition, a significant part of the arable land is cultivated in order to provide forage for game animals (Grönberg 2011).

### Analyses of nutrient composition

The full sample size ($n = 499$) was used for Near Infrared (NIR) spectroscopic analysis and associated modeling (see below), but 347 samples represented the seasons, years, areas and age-sex classes relevant for this paper (roe deer ($n$ = 61) and fallow deer ($n$ = 286) of both sexes, one year of age or older; Supplementary material Appendix 2, Table A3). No rumen samples were available for roe deer fawns and thus all juveniles of both species were excluded. Rumen content was collected year around from free ranging fallow deer and roe deer killed either during regular hunting and other times of the year, from road kills or through hunting with special permits (Gothenburg Board for Laboratory animals (Dnr: 405-2008) and Swedish Environmental Protection Agency (Dnr: NV-08702-12)). The hunting season for fallow deer lasts for males only during September and for both sexes from October to February, and for male roe deer from Mid-August to end of September and from October to January for both sexes. In this paper, we used data from animals killed during all months of the year 2006–2013. After removing the total intestine from the killed animal, the rumen was opened and the contents mixed to decrease effects of a structured content. A sample of 1 L per rumen was taken, representing 10–30% of the total rumen content (Kamler et al. 2003) and stored at −20 °C. For the sample preparation, all rumen samples were dried at 65°C. We used Near-infrared Spectroscopy (NIRS), as per Tigabu and Felton (2018), to predict the concentrations of different nutritional components, as this technique is rapid, nondestructive and accurate (Foley et al. 1998). Each pulverized rumen sample was thoroughly mixed before drawing ca. 40-g sample for scanning with XDS Rapid Content Analyzer (FOSS NIRSystems, Inc.). After scanning, 79 fallow deer samples representing a wide range of spectral variation and all of the 61 roe deer samples were selected for chemical analyses based on scores of Principal Component Analysis. These subsets of samples (140 in total) were analyzed for neutral detergent fiber (NDF), acid detergent fiber (ADF), ash, crude protein (CP), acid-detergent insoluble nitrogen (ADF-N), and lignin by using wet chemical analyses (methods described below). The calibration models were then developed for each nutritional fraction using absorbance values as regressor and chemical concentration of nutritive fractions as regressand. The model was validated using a prediction set, and then applied to predict the nutrition contents of the remaining samples (*n* = 359). Details of the methodology and model performance are given in Supplementary material Appendix 1.

We performed wet chemistry analyses to determine content of dry matter (DM), ash, CP, lignin, NDF, ADF, and acid-detergent insoluble N (ADF-N) of rumen samples (Van Soest et al. 1991; Table 1). All values of NDF and ADF are reported without residual ash (i.e., aNDFom and ADFom, respectively: Udén et al. 2005). ADF-N represents N attached to the ADF fraction of the plant that is unavailable for digestion and absorption (McDonald et al. 2011) and was measured in order to estimate the protein fraction available (AP) to the animal, i.e., available N from ingested forage that is by the time of sampling still not degraded. AP was calculated as total N times a conversion factor of 6.25 subtracted by ADF-N (Licitra et al. 1996). It is important to note that an unknown proportion of our measured AP will be microbial N (Van Soest 1994; Supplementary material Appendix 3). Both microbial N and N sourced directly from ingested forage contribute to the ruminant's protein content. However, the proportion between the fractions when they are absorbed later on in the digestive tract is not the same as in the rumen sample (Van Soest 1994). In lack of better data, we denote (total N minus ADF-N) as available protein (AP) for rumen samples, even if the indigestible part of microbial N (typically 15%) is not identified by ADF-N analysis contrary to indigestible feed protein (Van Soest 1994). Sample preparations and chemical analyses were performed by Agrilab AB, in Uppsala, Sweden (www.agrilab.se; Table 1). The proportion of cellulose (ADF–ADL) and hemicellulose (NDF–ADF) were then calculated. Instead of chemically analyzing total nonstructural carbohydrates (TNC) and lipid in rumen contents, we estimated these by subtraction (TNC + lipid = (100 – (NDF + AP + ash)); Irwin et al. 2014). The TNC fraction includes starch, sugars, and soluble nonstarch polysaccharides. The concentrations of fat are normally relatively low in the natural forage of deer at this latitude (1–3% of DM), compared to TNC (5–25% DM; Felton et al. 2016, Wam et al. 2018).

## Statistical analysis

Concentration of protein and mineral in plants, as well as digestible fiber (cellulose and hemicellulose) and lignin, can be significantly correlated to each other (Van Soest 1994; Felton et al. 2009; Felton et al. 2018), which can make it difficult to separate these constituents from each other. Therefore, we used simple correlation matrix (Spearman correlation) to analyze the relationships between AP and minerals (ash), as well as cellulose, hemicellulose, and lignin.

### Interspecific comparisons across seasons and area

All rumen samples were divided into the season each animal was killed by the following definition: spring (1st April–31st May), summer (1st June–30th September), fall (1st October–15th December), and winter (16th December–30th March). We used two-way ANOVA (type II or type III when appropriate for unbalanced data) between roe deer (*n* = 59) and fallow deer (*n* = 286) across seasons and FDD. Each model was first run with contrasts to check for interactions. If significant interactions where present, contrasts were removed from the model for trustful significance testing in ANOVA type III. If no significant interactions where present, contrasts and interactions were removed from the model and ANOVA type II was used. Analyses were followed by calculation of least-squares means with adjusted *P* values by the Tukey–Kramer method between roe deer (*n* = 59) and fallow deer (*n* = 286) across seasons and area, respectively. Interaction terms are not reported unless significant ($P < 0.05$). Residuals were checked for normality and homogeneity of variance across groups by visual examination of fits vs. residual plots. All data were logit transformed. One outlier (roe deer) was excluded from the dataset (residual > 6*IQR), with an AP value of 649 g $kg^{-1}$ DM, which was 33% higher compared to the second highest value of 495 g $kg^{-1}$ DM. The reason for that extreme value is not known, but must obviously be an anomaly. The removal of one outlier did not change the main result or conclusion of this paper. In addition, one sample (roe deer) was removed from further

**Table 1** Methods for chemical analyses of the nutritive fractions including their components, used in this study of rumen contents from roe deer and fallow deer at Koberg, southwestern Sweden, 2006–2013

| Fraction | Components | Method |
|---|---|---|
| DM | Dry matter | KLK 1965:1 |
| Ash | Inorganic constituents e.g., minerals and silica | KLK 1965:1 |
| CP (total N × 6.25) | Nitrogen from protein and nonprotein nitrogen (e.g., amino acids, urea, ammonia) | Dumas method according to ISO (13878:1998) |
| NDF | Cellulose, hemicellulose, and lignin i.e., cell wall material | van Soest et al. (1991) |
| ADF | Cellulose, lignified nitrogen, lignin, and silica | van Soest et al. (1991) |
| ADF-N | N attached to the ADF fraction | ISO (13878:1998) |
| ADL | Crude lignin | van Soest et al. (1991) |

analyses due to lacking information about geographical origin. The statistical models for each nutrient were thus based on 345 samples collected in the northern low FDD-area (*n* = 24 roe deer and *n* = 102 fallow deer rumen samples) and in the southern high FDD-area (*n* = 35 and *n* = 184), respectively (Supplementary material Appendix 2, Table A3). The proportion of available protein, cellulose, hemicellulose, lignin, and TNC were used as dependent variables in the analyses. Statistical analyses were done in RStudio (Version 1.1.456) using the packages Rmisc (Hope 2013), Hmisc (Harrell Jr 2020), stats (R Core Team 2020), base (R Core Team 2020), lsmeans (Lenth 2016), and car (Fox and Weisberg 2011).

## Results

### Interspecific variation in nutrient composition

Ash was positively correlated with AP in the rumen contents in this study (r = 0.37, $P < 0.0001$). Cellulose (r = 0.43, $P < 0.0001$) was positively correlated to lignin. Similarly, cellulose was positively correlated to hemicellulose (r = 0.27, $P < 0.0001$). Hemicellulose was positively correlated to lignin (r = 0.16, $P = 0.0023$). The overall nutrient composition of the two deer species' rumen contents is described in Supplementary material Appendix 2, Table A4.

A two-way ANOVA was conducted to examine effects of species, season, and area on different nutritive fractions. The main effect analysis showed a significant effect of species ($F_{1;\ 339} = 92.211$, $P < 0.0001$) and season ($F_{3;\ 339} = 78.489$, $P < 0.0001$; Fig. 1a) in terms of AP. The Tukey–Kramer test revealed that AP was significantly higher for roe deer compared to fallow deer in spring ($P = 0.0139$), summer ($P < 0.0001$) and winter ($P = 0.0003$) by 41%, 36% and 35% percentage points, respectively, but there were no significant differences between species in fall ($P \geq 0.46$). The variation ranged across seasons between 200 and 412 g $kg^{-1}$ DM for roe deer and 149 and 291 g $kg^{-1}$ DM for fallow deer. A disordinal interaction effect was found between species and season ($F_{3;\ 336} = 3.33$, $P = 0.02$; Fig. 1b; and Supplementary material Appendix 2, Table A5) in terms of lignin. The Tukey–Kramer test showed a significantly higher mean for fallow deer compared to roe deer in spring ($P = 0.016$) by 56% percentage points, but no significant differences between species in terms of lignin content in summer, fall or winter ($P \geq 0.40$, in all cases, Fig. 1b). The variation in lignin across seasons ranged between 58 and 140 g $kg^{-1}$ DM for roe deer and 90 and 147 g $kg^{-1}$ DM for fallow deer. Main effect analyses of cellulose content showed a significant effect of season ($F_{3;\ 339} = 42.89$, $P < 0.0001$) and species ($F_{1;\ 339} = 11.43$, $P < 0.0001$; Fig. 1c; Supplementary material Appendix 2, Table A5). The variation in cellulose ranged across seasons between 122 and 233 g $kg^{-1}$ DM for roe deer and 144 and 252 g $kg^{-1}$ DM for fallow deer. No significant differences in cellulose content were found between species in spring, summer, fall or winter ($P \geq 0.22$; Fig. 1c). An ordinal interaction in hemicellulose content was found between species and season ($F_{3;\ 336} = 30.04$, $P < 0.0001$; Fig. 1d). The Tukey–Kramer test revealed that hemicellulose was significantly higher for fallow deer compared to roe deer in spring ($P < 0.0001$) and summer ($P < 0.0001$) by 177% and 35% percentage points, respectively, but there were no significant differences between species in fall ($P > 0.64$) or winter ($P > 0.89$). The variation ranged across seasons between 63 and 205 g $kg^{-1}$ DM for roe deer and 175 and 214 g $kg^{-1}$ DM for fallow deer. A tendency to disordinal interaction effect was found between species and season ($F_{3;\ 336} = 2.54$ $P = 0.057$; Fig. 1e) in terms of TNC. No significant differences were found between species in spring, summer, fall and winter ($P \geq 0.24$). The variation in TNC across seasons ranged between 128 and 213 g $kg^{-1}$ DM for roe deer and 136 and 176 g $kg^{-1}$ DM for fallow deer.

### Effects of high and low FDD on the variation in nutritional composition

The main effect analysis of AP content showed tendency toward an effect of area ($F_{3;\ 339} = 3.51$, $P = 0.062$; Fig. 2a; and Supplementary material Appendix 2, Table A5). The Tukey–Kramer test revealed a significantly higher mean for roe deer compared to fallow deer in the high FDD area ($P < 0.0001$) and low FDD area ($P < 0.0001$) by 55% and 36% percentage points, respectively. AP ranged from 254 g $kg^{-1}$ DM (low FDD) to 289 g $kg^{-1}$ DM (high FDD) for roe deer and were 187 g $kg^{-1}$ DM in both low and high FDD areas for fallow deer. No significant effect of area was found in lignin ($F_{3;\ 336} = 0.27$, $P = 0.60$; Fig. 3b) or cellulose content ($F_{3;\ 339} = 0.012$, $P = 0.91$; Fig. 3c). The mean variation in lignin content ranged between 96 g $kg^{-1}$ DM (high FDD) and 98 g $kg^{-1}$ DM (low FDD) for roe deer and 117 g $kg^{-1}$ DM (low FDD) and 125 g $kg^{-1}$ DM (high FDD) for fallow deer. Cellulose varied between 182 g $kg^{-1}$ DM (high FDD) and 204 g $kg^{-1}$ DM (low FDD) for roe deer and 214 g $kg^{-1}$ DM (low FDD) and 220 g $kg^{-1}$ DM (high FDD) for fallow deer. The main effect analysis of hemicellulose content showed a significant effect of area ($F_{1;336} = 13.58$, $P = 0.00027$; Fig. 3d). The Tukey–Kramer test revealed a significantly higher mean of hemicellulose for fallow deer compared to roe deer in the high FDD ($P < 0.0001$) and low FDD area ($P < 0.0001$) by 38% and 19% percentage points, respectively. The variation in hemicellulose content ranged between 149 g $kg^{-1}$ DM (high FDD) and 182 g $kg^{-1}$ DM (low FDD) for roe deer and 205 g $kg^{-1}$ DM (high FDD) and 217 g $kg^{-1}$ DM (low FDD) for fallow deer. The main effect analysis of TNC content showed a significant effect of area

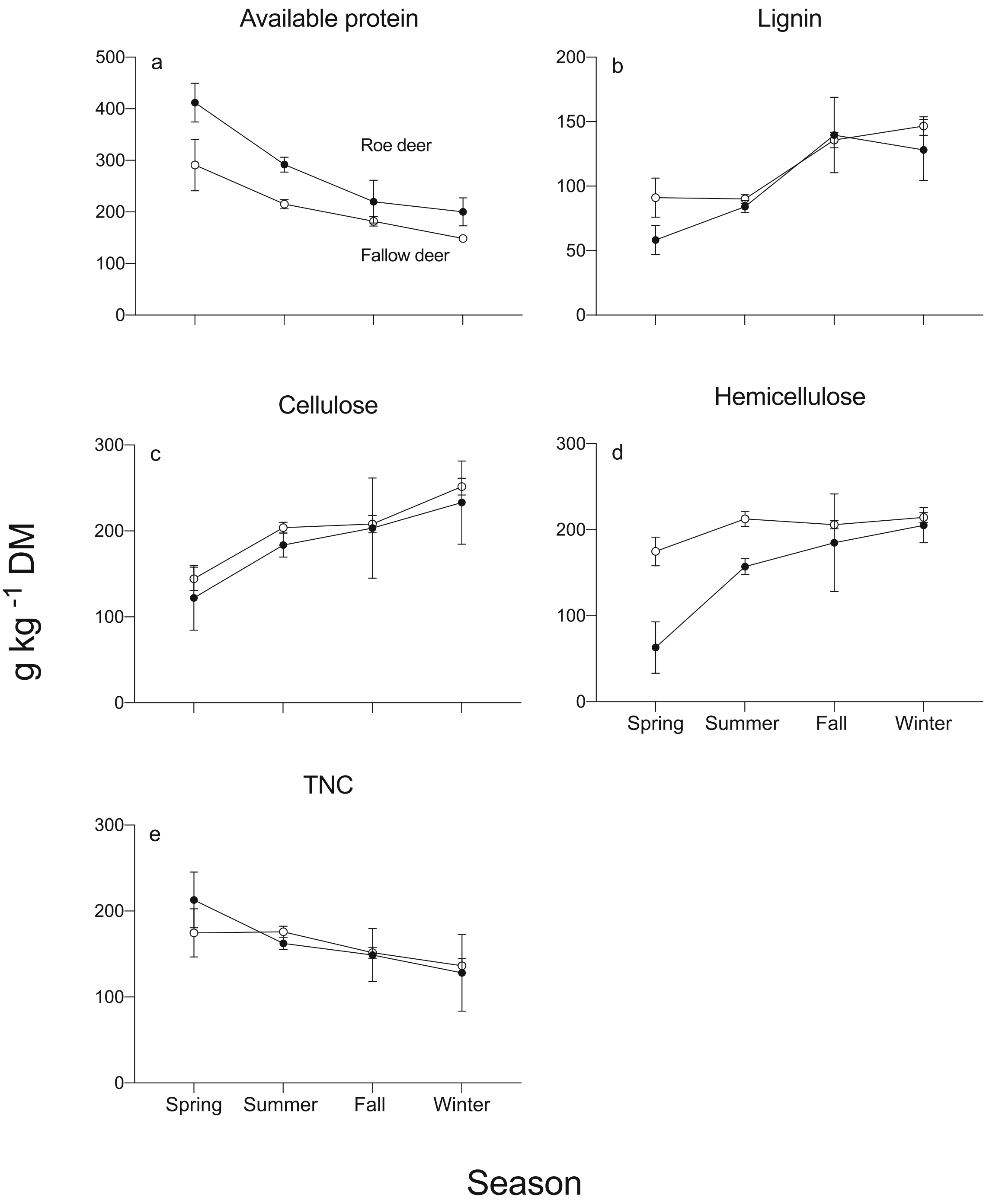

**Fig. 1** Proportion (g kg$^{-1}$ DM) of **a** available protein, **b** lignin, **c** cellulose, **d** hemicellulose, and **e** total nonstructural carbohydrates (TNC) in rumen samples of roe deer and fallow deer with comparisons between species. Dark gray marker points represent roe deer and light marker points represent fallow deer, with 95% confidence interval. Based on rumen samples from animals killed at Koberg, southwestern Sweden, 2006–2013

($F_{1;336}$ = 5.54, $P$ = 0.019; Fig. 2e), but the Tukey–Kramer test revealed no significant differences between mean of TNC for fallow deer compared to roe deer in the high FDD ($P$ = 0.97) and low FDD area ($P$ = 0.95). TNC varied between 154 g kg$^{-1}$ DM (low FDD) and 160 g kg$^{-1}$ DM (high FDD) for roe deer and 151 g kg$^{-1}$ DM (high FDD) and 165 g kg$^{-1}$ DM (low FDD) for fallow deer.

## Discussion

This study produced three key results. First, using rumen content composition as a proxy, we show that the nutritional composition of roe deer and fallow deer diets varied among seasons, with the greater seasonal variation observed in roe deer. Second, the nutritional composition of diets varied between

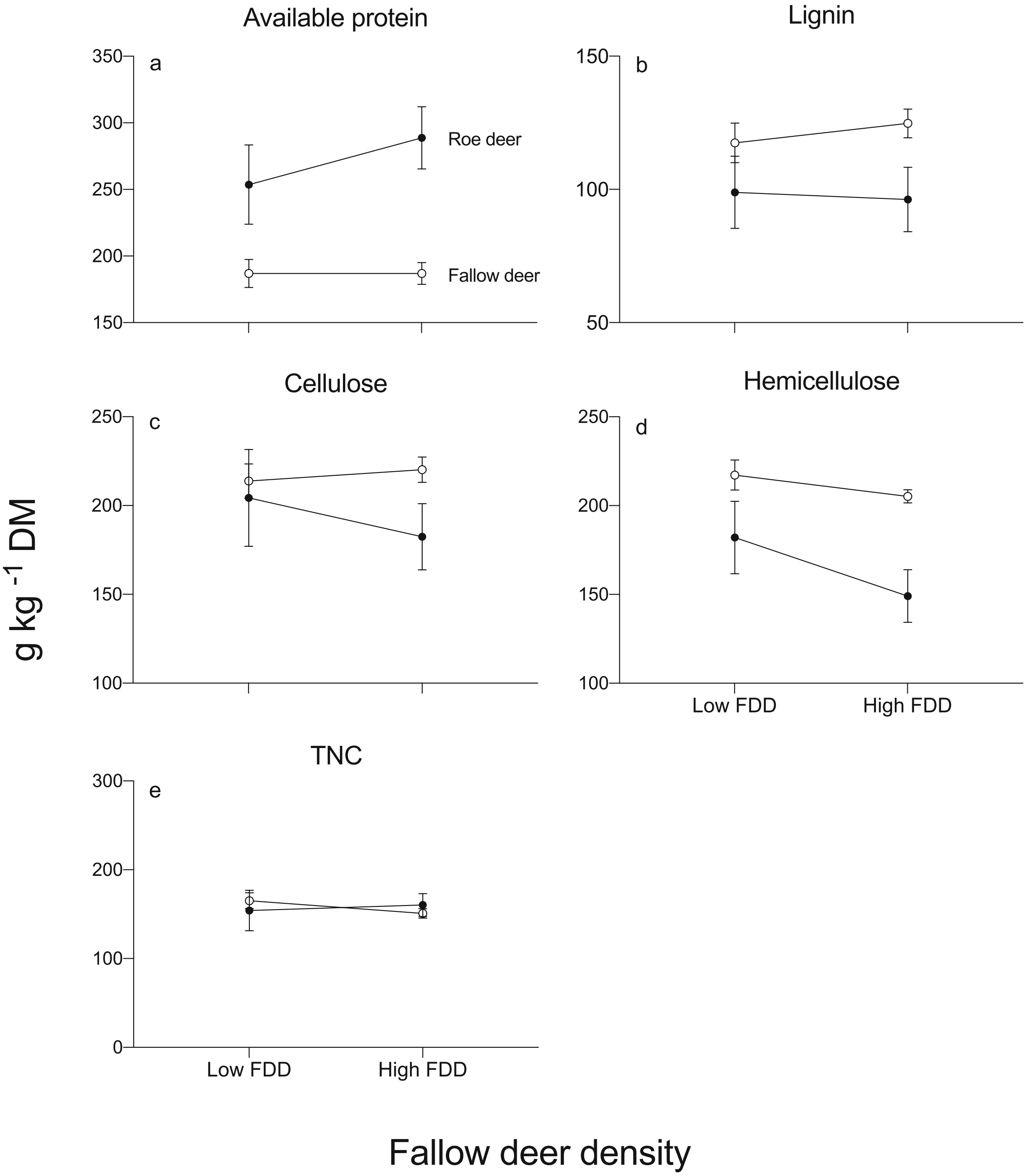

**Fig. 2** Proportion (g kg$^{-1}$ DM) of **a** available protein, **b** lignin, **c** cellulose, **d** hemicellulose, and **e** total nonstructural carbohydrates (TNC) in rumen samples of roe deer and fallow deer with comparisons between two parts of the study area; North = low density of fallow deer and South = high density of fallow deer. Dark gray marker points represent roe deer and light marker points represent fallow deer, with 95% confidence interval. Based on rumen samples from animals killed at Koberg, southwestern Sweden, 2006–2013

the two species, with roe deer (the browser) having consistently lower proportions of digestible fiber (particularly hemicellulose) and higher proportions of available protein (AP) in their rumen contents compared to fallow deer (the intermediate feeder), although the level of significance differed across seasons. Thus, we found support for two of our postulated predictions. Finally, our comparison of the nutritional composition of rumen contents under two contrasting densities of fallow deer suggest, in line with our prediction, that the effect of niche differentiation may be amplified under conditions of relatively high competition compared to low levels, although the effect of density was not significant for all nutrients analyzed. Below we will discuss these results in more detail.

At northern latitudes, as plants mature and develop after summer solstice toward winter, there is normally a clear decline in plant protein and energy content, while the relative content of polysaccharides (cellulose, hemicellulose) and lignin increase, resulting in declining digestibility, and hence, declining nutritive value of plants (Jarman 1974; Van Soest 1996). The seasonal variation in estimated nutrient composition of deer rumen content in our study is similar to the seasonal cycle of roe deer found by König et al. (2020) and Kamler et al. (2011) The proportion of available protein in our rumen samples varied accordingly across seasons, with the lowest levels in winter for both roe deer (mean 200 g kg$^{-1}$ DM) and fallow deer (mean 149 g kg$^{-1}$ DM) and the highest levels in spring (mean 412 g kg$^{-1}$ DM for roe deer and mean 291 g kg$^{-1}$ DM for fallow deer). Similarly, the concentrations of readily digestible and energy-providing carbohydrates (TNC) in rumen samples also declined from spring to winter (with no significant differences between the two species). We therefore believe that this pattern reflects the expected variation in nutrient intake across seasons (Leslie et al. 1984), a pattern further supported by the increasing proportions of cellulose, hemicellulose and lignin that we observed from spring to winter (Fig. 1).

Although our data on how plant nutrient levels develop across seasons show a general and expected pattern, there were clear differences between deer species in their respective patterns. Roe deer had a significantly higher proportion of AP in their rumen contents than fallow deer in spring, summer, and winter. There was, however, no significant differences were found in fall between species, which is likely to be an outcome of the low-sample sizes of roe deer ($n = 5$) compared to fallow deer ($n = 88$). Similarly, there are low sample sizes also in spring for fallow deer ($n = 12$) and roe deer ($n = 5$). Another possible explanation for the nonsignificant differences of AP between the two species during fall could be that their diets in fact are overlapping to a greater extent during this season, or that different diets are similar in available protein. As an example, Obidziński et al. (2013) demonstrated that fall and winter diet of roe deer and fallow deer overlap by 60%, and similarly Latham et al. (1999) found that roe deer and red deer (*Cervus elaphus*) diets overlapped more in winter than during summer. In our study area (Koberg) macroscopic examination of 83 fallow deer and 26 roe deer rumen samples indicates a close to 75% diet overlap between the two species during winter (Kjellander et al. unpublished). The proportion of crude protein found in this study is higher than previously published values of forage protein content at northern latitudes (USA: Leslie et al. 1984, Switzerland: Moser et al. 2006, France: Verheyden-Tixier et al. 2008). This is not surprising considering that our measure of CP includes microbial nitrogen as well and cannot therefore be directly compared with the plants' contents (see Supplementary material Appendix 3). Our results are more similar to previous results obtained from roe deer rumen samples in Serbia and southern Germany (Djordjevic et al. 2006; Popovic et al. 2009; König et al. 2020), although our samples exceed these values. In these studies, the CP content of roe deer rumen samples in spring reached 344–374 g kg$^{-1}$ DM and in our results the mean CP content was 433 g kg$^{-1}$ DM of roe deer in spring. Importantly, because of a more explosive vegetation spring flush, cell soluble (protein and TNC) content is expected to be higher at higher latitudes (e.g., Sweden vs. Serbia and Germany) due to differences in temperature and photoperiod, with subsequent differences in plant growth and composition (Klein 1990; Myneni et al. 1997). However, the relatively high concentrations of AP in our samples could merely be a result of coincidence considering the low sample sizes for roe deer ($n = 5$) in spring (Supplementary material Appendix 2, Table A3).

Our finding that roe deer had significantly higher proportion of AP in their rumen contents than fallow deer is in line our second prediction based on their morpho-physiologic adaptations and associated foraging niches (Hofmann 1989). The differences in energy utilization (Andersen et al. 2000) and nutritional requirements may also vary between species due to differences in reproductive strategies. Among ungulates, energy requirements are highest during gestation and lactation (Oftedal 1985; Parker et al. 2009), but strategies to allocate body reserves vary among species. Income breeders generally rely on current resources and accumulate less body reserves whereas capital breeders utilize stored energy (fat and protein) for reproduction (Jönsson 1997). In addition, females of a species giving birth to several offspring (polytocous species) generally have higher energy and protein requirements compared to females giving birth to only one (monotocous species, National Research Council 2007). Roe deer is a typical polytocous income breeder (Andersen et al. 2000) giving birth to 1–4 fawns, in late May to early June, coinciding to a large extent with the time males establish mating territories (Liberg and Wahlström 1995; Andersen and Linnell 1997). In contrast, fallow deer belongs to the continuum of capital breeder and is a clear monotocous species, usually giving birth to only one fawn in mid to late June (Birgersson and Ekvall 1997; Kjellander et al. 2012). Even if our estimated rumen protein concentrations in the two species do not reflect the animals' requirements in absolute terms, a discussion of additional influencing factors (not assessed in this study) with regards to differentiated requirements between the two species may be warranted. For example, the timing of peak protein requirements relative to body weight differs between the two species. Male roe deer establish mating territories during late spring and females give birth approximately one month earlier than fallow deer i.e., late May vs late June (Kjellander et al. 2012). This may influence the demand of highly digestible feeds for roe deer, which in turn may influence the amount of AP found in the rumen samples.

Our results suggest that both roe deer and fallow deer were limited to a diet higher in digestible fiber (hemicellulose and cellulose) during winter, likely due to a gradually depleting food resource after a completed vegetation season, and the physiochemical changes in the forage. The content of hemicellulose in forbs, tree twigs and shrubs generally increases with maturity (McDonald et al. 2011; Felton et al. 2018), and graminoids' cellulose content can increase with 50% from spring to winter (Leslie et al. 1984; Moser et al. 2006). While we did not find a significant difference in rumen cellulose content between the two species in any season, the proportion of hemicellulose was significantly higher for fallow deer compared to roe deer during the growing season, and remained relatively stable for fallow deer across seasons. In roe deer rumens, hemicellulose was lowest in spring and increased gradually to the highest proportions in winter. It is likely that the roe deer were able to avoid high hemicellulose content forage in spring when forbs dominate their diet (up to 90%), but less so later in summer as the forage wither or go into winter dormancy (Cederlund et al. 1980; Gębczyńska 1980; Obidziński et al. 2013; Nichols et al. 2016). Roe deer in the boreal system select dwarf-shrubs in fall and beginning of winter at a snow depth less than 50 cm but are forced to a diet dominated by dormant twigs from taller plants at greater snow depths (Cederlund et al. 1980).

The lack of significant difference between deer species in terms of rumen cellulose concentrations contradicts the general prediction that fallow deer should ingest a higher proportion cellulose than roe deer due to higher cellulolytic fermentation capability irrespective of body weight (Prins and Geelen 1971; Hofmann 1989), and may be due to the small sample sizes of roe deer in our study (as indicated by the high confidence interval). Overall, cellulose and hemicellulose concentrations in rumen samples were positively correlated with each other. Roe deer in our study area are known to eat less graminoids compared to fallow deer (Nichols et al. 2016), and other studies have shown that roe deer' intake of graminoids is low, ranging between 3.8% (winter) and ca 9% (growing season) (Cederlund et al. 1980; Gębczyńska 1980; Obidziński et al. 2013; Spitzer et al. 2020). In contrast, there are several studies showing that the diet of fallow deer is frequently dominated by graminoids (e.g., Putman 1986; Poli et al. 1996; Obidziński et al. 2013; Nichols et al. 2016), but sometimes it is dominated by trees or shrubs (Bruno and Apollonio 1991; Poli et al. 1996) or acorns (Morse et al. 2009). There is, however, a large variation in the chemical composition among species included in the vastly diverse morphological group we call graminoids (including the families *Poaceae*, *Cyperaceae*, and *Juncaceae*), and more research is needed to discern whether our result is a sampling artifact or a result of diet composition.

While cellulose and hemicellulose are the main fuel for ruminants, typically providing up to 80% of their energy (Barboza et al. 2008), the third structural carbohydrate, lignin, is indigestible to them. However, lignin provides structure in the rumen necessary for microbial processes (Van Soest 1994). Hence, while browsers are expected to select material with greater digestibility (less lignin) than intermediate feeders, at least during the growing season, lignin, as well as the other structural carbohydrates, is an unavoidable component of the diets of both species (Felton et al. 2018). We found that, as predicted, the proportion of lignin was significantly higher for fallow deer compared to roe deer, but only during the spring. It is possible that fallow deer, like white-tailed deer (also an intermediate feeder), tolerate larger proportions of lignin in their diet only as long as the concentration of cell solubles in the forage is relatively high (Daigle et al. 2004). Lignin content in roe deer rumens in our study was relatively low (130 g kg$^{-1}$ of rumen DM in winter) compared to a previous study of roe deer in Norway where lignin reached 180 g kg$^{-1}$ of rumen DM in winter (Holand 1992). This is likely explained by diet variation between the study sites, as in plants, lignin content can vary greatly between herbs and deciduous trees in winter (Moser et al. 2006).

When comparing the composition of rumen contents between high and low FDD areas, the results revealed that some aspects of rumen nutritional composition differences were greater between roe deer and fallow deer in the high FDD area compared to the low FDD area. This is also what we expect based on our third prediction, since a relatively higher FDD may influence roe deer to eat different foods, or to combine foods at different amounts, than at low FDD. At high FDD, roe deer had higher AP and lower hemicellulose in rumen contents compared to fallow deer, suggesting that niche partitioning occurs when FDD increases. These results are in line with the concept that competing sympatric species are expected to develop niche differentiation to avoid or decrease competition (and thus minimize resource overlap) as long as resources are not limiting (Pianka 1974; Schoener 1974), especially at higher densities (Svärdson 1976). However, the effect of density in our study was not significant for lignin or cellulose. Several previous studies have suggested niche separation for coexistence of competing sympatric ungulates (Krämer 1973; Hanley and Hanley 1982; Whitney et al. 2011; Torres et al. 2012; Pokharel et al. 2015). Still, our results are in clear contrast to Stewart et al. (2011) since they found dietary overlap to be increased between sympatric mule deer (*Odocoileus hemionus L.*) and North American elk (*Cervus elaphus L.*) at high elk densities. Further research is needed to clarify the effect of interspecific competition on nutritional niche separation between these two deer species.

In conclusion, the comparisons of rumen nutrient composition showed that levels of macronutrients differed between species and across seasons. Furthermore, the roe deer, a species that is adapted to early successional habitats offering relatively nutritious resources, appears to have a more differentiated nutritional composition of rumen contents under high densities of fallow deer. Competition is a driving force in evolutionary adaptations that can induce niche separation and is expected to be further enhanced in areas where native and exotic species coexist, and we thus suggest that the differences between the native roe deer and introduced fallow deer in this study could be explained by niche separation as long as resources are not too limited (such as in winter). Knowledge about different foraging adaptations can thus be used to better understand diet overlap and inter- and intraspecific competition.

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**Availability of data and material** We intend to make data accessible via Dryad if our manuscript becomes accepted.

**Author contribution** PK conceived and designed the experiments. HR and AF designed and performed lab analyses. HR, AF, and UAB analyzed the data, and HR drafted the manuscript. PK and UAB received grants for the analyses. PK, AF, and UAB contributed to the writing of the manuscript. MT performed the NIRS analyses. All authors approved the final version.

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## Declarations

The management, preservation, and accessibility of all data generated in this project will be handled according to SLU guidelines as adapted from the EDINA-project, University of Edinburgh.

**Ethics approval** All applicable institutional and/or national guidelines for the care and use of animals were followed. The methods used in this study comply with the current laws of Sweden. We obtained ethical permissions from the Gothenburg Board for Laboratory animals (Dnr: 405-2008) and Swedish Environmental Protection Agency (Dnr: NV-08702-12).

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Conflict of interest** The authors declare that they have no conflict of interest.

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