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ORIGINAL ARTICLE

Assessing the influence of body size on patterns of dietary niche segregation among the ungulate community in Yellowstone National Park, USA

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Abstract

Evaluating the factors that promote coexistence between ecologically similar species is crucial to understanding the evolution and assembly of herbivore communities. The Jarman–Bell principle presents a trade-off between diet quality and quantity as an axis for dietary niche segregation and has been suggested as a mechanism facilitating species coexistence. This idea holds that larger-bodied herbivores consume greater amounts of relatively low-quality plant resources, while smaller-bodied herbivores typically feed selectively on higher-quality resources. Most studies investigating the Jarman–Bell principle have examined free-living ungulates in African savannas. The diverse ungulate community in Yellowstone National Park, USA offers an opportunity to investigate the applicability of this principle in a temperate North American ecosystem. In this study we use fecal nitrogen (FN) and stable carbon isotope values ($\delta^{13}C$) to examine the relationship between body size and seasonal patterns of dietary niche segregation among five species of wild ungulates. Specifically, we test the predictions that: (1) diet quality decreases with increasing body mass, (2) interspecific differences in diet are greatest between the largest- and smallest-bodied species, and (3) smaller-bodied species have narrower dietary breadth than larger-bodied species. Diet quality, as indicated by digestibility, declined significantly with body mass, consistent with the empirical pattern predicted by the Jarman–Bell hypothesis. Significant interspecific differences in diet quality generally aligned with variation in body mass. When resources were limited during the winter, the relationship between body mass and diet quality was more pronounced, suggesting increased dietary niche segregation during the lean season. The results showed little evidence indicating that dietary breadth scaled allometrically with body mass, as the two species most similar in body mass displayed the greatest and least range of seasonal variation in both FN and $\delta^{13}C$. This study adds to the weight and breadth of evidence that diet quality is negatively correlated with body size in wild ungulate assemblages. Our findings underscore the importance of body size as a factor facilitating dietary niche segregation and promoting coexistence among ecologically similar ungulate species.

Keywords Dietary niche segregation · Body size · Ungulates · North America

Introduction

The remarkable level of species diversity in ungulate communities is often explained through a framework of dietary niche segregation, wherein differences in the diets of sympatric species promote coexistence by reducing interspecific competition (Schoener 1974; Jarman and Sinclair 1979; Belovsky 1986). Evaluating the underlying mechanisms that facilitate segregation in a group of herbivores utilizing a broadly similar range of plant resources is key to understanding community assembly and function (Lamprey 1963; MacArthur and Levis 1967; McNaughton and Georgiadis 1986). Most research has focused on differences in either diet type or quality when investigating segregation, and a range of traits including body size, digestive morphophysiology, and craniodental anatomy have been functionally linked to both variables (Bell 1970; Hofmann and Stewart 1972; Jarman 1974; Demment and Van Soest 1985; Hofmann 1989; Gordon and Illius 1994; Clauss et al. 2007,

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2013; Kaiser et al. 2013; Dittmann et al. 2015; Lazagabaster et al. 2016). Diet type-based models typically consider the proportion of grass consumed, with grazers consuming mostly grasses, browsers consuming mostly non-grasses, and intermediate feeders consuming both, resulting in a grazer-browser continuum (Lamprey 1963; Cerling et al. 2003; Codron et al. 2007). Separately, models focused on diet quality highlight the trade-offs between the quantity and nutritional quality of plants consumed (Bell 1971; Jarman 1974). In this study, we use fecal nitrogen (FN) and stable carbon isotope values ($\delta^{13}C$) to evaluate patterns of dietary niche segregation within the ungulate community in Yellowstone National Park (YNP), USA. Specifically, we investigate whether differences in body size predict variation in diet quality or breadth.

Body size is a fundamental biological trait determining many ecological, behavioural, and physiological characteristics of an animal (Bell 1970; Jarman 1974; Demment and Van Soest 1985; Fritz and Loison 2006; Hopcraft et al. 2010). The Jarman–Bell principle (JBP) emphasizes the relationship between body size and dietary quality, predicting that large-bodied species consume greater amounts of low-quality forage, while smaller-bodied herbivores feed selectively on higher-quality resources (Bell 1971; Jarman 1974; du Toit and Olff 2014). Here diet quality refers to the nutritional value of food as defined by protein and/or digestible-energy content. Metabolic rate allometries, specifically the putative scaling of basal metabolic rate ($\approx M^{0.75}$) and food retention time ($\approx M^{0.25}$), were long thought to underpin the relationship between body size and diet quality (Demment and Van Soest 1985; Illius and Gordon 1987). Research over the past decade, however, has shown that while the body size—diet quality relationship is empirically common (Clauss et al. 2013; Arman and Prideaux 2015; Garnick et al. 2018; Potter et al. 2022; Daskin et al. 2023), it cannot be explained simply on the basis of physiological allometries (Clauss et al. 2013; Müller et al. 2013; Steuer et al. 2014). Other mechanisms put forth to explain the JBP can be broadly divided into those focused on digestive physiology, evolutionary factors, and ecological trade-offs (review in Potter and Pringle 2023), with ecological trade-offs being the most widely accepted in the literature (Clauss et al. 2013; Codron 2019). Most studies examining the JBP in free-ranging ungulates have been conducted in African savannas (Bell 1971; Jarman 1974; Jarman and Sinclair 1979; Sensenig et al. 2010; Kleynhans et al. 2011; Potter et al. 2022). The diverse ungulate community in YNP offers an opportunity to evaluate the JBP in a temperate North American ecosystem.

Biochemical analysis of feces is often utilized in wildlife research due to the non-invasive nature of sample collection and proven effectiveness for evaluating diet with respect to both space and time (Codron et al. 2007, 2013; Leslie et al. 2008; Codron and Codron 2009). FN is composed of a large proportion of metabolic fecal nitrogen (both microbial and endogenous in origin) and a smaller proportion of food residue nitrogen (Wehausen 1995; Schwarm et al. 2009; Steuer et al. 2014). Metabolic nitrogen increases with the proportion of readily fermentable carbohydrates consumed and has been shown to be highly correlated with FN (Leite and Stuth 1995). The correlation between FN and metabolic fecal nitrogen has fostered the use of FN as an index of dietary quality since the 1940s (Lancaster 1949; Holecheck et al. 1982; Leslie et al. 2008; Verheyden et al. 2011; Galvez-Ceron et al. 2015; Espunyes et al. 2022). The concentration of FN is typically higher when there are less indigestible substances in the diet (e.g., indigestible fibre) and more substrates on which intestinal microbes can grow (e.g., digestible fiber and carbohydrates) (Schwarm et al. 2009). Studies of wild ungulates have demonstrated a positive relationship between FN and elevation that has been linked to plant phenology and used to track changes in diet quality during seasonal migration (Van Soest 1983; Festa-Bianchet 1988; Albon and Langvatn 1992; Sakuragi et al. 2003). While FN provides an effective, albeit coarse, proxy for diet quality, its interpretation must be accompanied by several caveats. First, the relationship between diet quality and FN can be obfuscated when the diet includes a large proportion of secondary plant compounds, such as tannins. When herbivores consume large quantities of tannins, the FN concentration can become elevated because tannins make dietary nitrogen partly indigestible (Hobbs and Hanley 1990). However, this tannin-mediated decoupling of the relationship between FN and diet quality appears limited to browsers and cases where animals ingest unusually high amounts of secondary plant compounds (Leslie et al. 2008; Verheyden et al. 2011; Carpio et al. 2015). Second, FN is an indicator of diet quality linked to overall digestibility (Clauss et al. 2013), which is often, but not always, higher in diets that are higher in protein. An experimental study by Steuer et al. (2014) showed that while body size was negatively correlated with digestibility in free-ranging ungulates, it did not influence digestibility in captive ungulates fed a consistent diet. In nature, higher-protein forage is typically more digestible, however, because protein content and digestibility can vary widely, comparing FN across feeding types (e.g., grazer vs. browser) can be problematic. Finally, the third caveat involves intraspecific variation in FN occurring in association with differences in age, body mass, sex, reproductive status, and body condition (Čupić et al. 2021). Because these factors cannot always be readily assessed when studying free-ranging ungulates, interpretations of diet quality based on FN can be misleading.

Animals that feed on different kinds of plants will reflect the carbon isotope ratio ($^{13}C/^{12}C$) that was ingested in their body tissues and faeces. Studies using $\delta^{13}C$ to investigate the diet of sympatric ungulates have predominantly focused on xeric and tropical ecosystems where pronounced contrasts in isotopic values exist between grazing and browsing species (Quade et al. 1992; Tieszen 1994; Cerling et al. 1999; MacFadden et al. 1999; Codron et al. 2007). In these ecosystems, grazers consume grass and other graminoids that use the C_4 photosynthetic pathway, while browsers eat leaves of trees and shrubs that use the C_3 photosynthetic pathway. However, vegetation in temperate and boreal ecosystems is dominated by C_3 plants (Still et al. 2003; Lüttge 2004). In YNP, for example, up to 97% of all plant taxa use the C_3 photosynthetic pathway (Teeri and Stowe 1976; Stowe and Teeri 1978; Sage et al. 1999). $\delta^{13}C$ can still be used to investigate herbivore diet in C_3-dominant ecosystems because of predictable variations in the $\delta^{13}C$ values of plants occurring due to differences in aridity, soil salinity, degree of canopy cover, carbon source (atmospheric or aquatic), nitrogen source, and mycorrhizal associations (Tieszen 1991; Lajtha and Michener 1994; Hare et al. 2018). In forested environments, poor ventilation of the understory, depleted CO_2 resulting from the decomposition of leaf litter, and decreased solar radiation, result in a spectrum of plant $\delta^{13}C$ values from more depleted under the shade-crown dense canopy (Van der Merwe and Medina 1991), to less depleted in more open canopy habitats (Francey and Farquhar 1982). Different plant parts can reflect widely varying $\delta^{13}C$ values due to different formation times, biochemical composition, fractionations during transportation of biomolecules within the plant, and height within the forest canopy (Chevillat et al. 2005; Cernusak et al. 2009; Ghashghaie and Badeck 2014). For example, lower $\delta^{13}C$ values are typically associated with plant leaves relative to seeds/flowers (Badeck et al. 2005; Metcalfe and Mead 2019). Several studies have shown an increase in the $\delta^{13}C$ values of C_3 plants with elevation (Morecroft and Woodward 1990; Li et al. 2006, 2007, 2009; Liu et al. 2016) that can be recorded in the $\delta^{13}C$ values of livestock tissues (Männel et al. 2007). This pattern has been explained by the high carboxylation rates relative to stomatal conductance at higher elevations, which results in lower $\delta^{13}C$ discrimination (Morecroft and Woodward 1990; Li et al. 2006, 2007, 2009). The combined effect of plant-part and habitat selection can result in significant carbon isotope niche segregation within C_3-dominant environments, with the largest differences between animals consuming seedy/flowering plants in open canopy habitats (higher $\delta^{13}C$), and those selecting seedless/flowerless plants in closed canopy habitats (lower $\delta^{13}C$). While interspecific variation in herbivore $\delta^{13}C$ is typically far less pronounced in C_3-dominant ecosystems, significant differences in diet and microhabitat use have been demonstrated (Cerling et al. 1999, 2004; Stewart et al. 2003; Urton and Hobson 2005; Feranec 2007; Krigbaum et al. 2013; Tejada et al. 2020). Within the YNP ecosystem, we use ungulate fecal $\delta^{13}C$ as an indicator of variation in habitat use and plant types/parts consumed.

Using FN and $\delta^{13}C$ we test the following predictions: (1) diet quality, as indexed by FN, will decrease with increasing body size across the sampled species; (2) interspecific differences in FN and $\delta^{13}C$ will be greatest between the largest- and smallest-bodied species; and (3) smaller-bodied species will have narrower dietary breadth, as indexed by lower intraspecific variability in FN and $\delta^{13}C$, than larger-bodied species. To investigate the influence of seasonality on patterns of dietary niche segregation we analyze FN and $\delta^{13}C$ during both summer when resources are abundant and winter when they are scarce. To evaluate spatial differences in diet we analyze the relationship between elevation and FN and $\delta^{13}C$ values. The five YNP ungulate species examined in this study include bison (*Bison bison*), elk (*Cervus canadensis*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and mule deer (*Odocoileus hemionus*). Testing the relationship between diet quality and body size in a temperate North American ecosystem offers important information for understanding the environmental and taxonomic generalizability of the JBP. Additionally, a greater awareness of the mechanisms facilitating dietary niche segregation among ecologically similar ungulate species will allow wildlife managers to augment resource availability based on the composition of local communities.

Material and methods

Study area

Yellowstone National Park occupies 8991 km^2 of primarily forested (~ 80%) habitat in northwestern Wyoming, extending into Idaho and Montana, USA, and ranges from 1500 to 3300 m in elevation (44°25′47″N and 110°35′4″W). The park is at the core of the Greater Yellowstone Ecosystem, which represents one of the last remaining large (89,000 km^2), nearly intact ecosystems in the northern temperate zone. The climate is characterized by long, cold winters (daily mean ≈ – 10 °C) and short, cool summers (daily mean ≈ 10 °C), resulting in a mean annual temperature of 3 °C. A snowpack typically accumulates from November, peaking in April, and ablating completely by June. Seasonal fluctuation in temperature and precipitation produces predictable vegetation patterns (Marston and Anderson 1991). Forest tree species are dominated (95%) by lodgepole pine (*Pinus contorta*) differentiated primarily on the basis of successional stage. Non-forested habitats include expansive dry sagebrush-grassland steppe, wet willow-sedge meadows, areas of geothermal activity, and alpine tundra at the highest reaches of all major mountain ranges (Waddington and Wright 1974; Despain 1990).

A diversity of native large ungulates reside within YNP including elk, bison, mule deer, pronghorn, bighorn sheep, white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and mountain goat (*Oreamnos americanus*). The five species evaluated here were selected because they vary in body size and represent the most abundant ungulate species in the park. Each of the studied species are migratory moving seasonally throughout the park, and in some cases, beyond its boundaries. With focus to the habitat preferences of the studied species, elk and mule deer are associated with a variety of overlapping habitats including pine forest, wet meadows, and sagebrush-grassland-steppe. Bison and pronghorn typically occupy sagebrush-grassland-steppe habitats. Finally, bighorn sheep are associated with alpine and subalpine habitats in the upper Yellowstone River drainage (Merrill and Boyce 1991; Singer and Norland 1994). Wolves (*Canis lupus*) were extirpated from YNP by the mid-1920s, absent for a period of seven decades, and reintroduced in the winters of 1995/1996, creating a natural experiment through time and an opportunity to study cascading trophic interactions (Smith and Ferguson 2012). Rapid recovery of the wolf population caused both temporal and spatial variability in wolf-ungulate interactions and likewise coincided with significant temporal and spatial variation in the vegetation (Ripple and Beschta 2012; Boyce 2018). The fecal samples analyzed in this study were collected during the summer and winter seasons of 2002–2004, offering a window into ungulate diets less than a decade after wolf reintroduction.

Sample collection and analysis

Fecal samples analyzed in this study were collected from five species of ruminants inhabiting YNP during August 2002, August 2003, and January 2004 (Table 1). $\delta^{13}C$ data from August 2002 evaluated here are the same as those reported by Feranec (2007). An average of 15 samples per species were collected each season from a range of habitats throughout the park. The spatial distribution of samples was dependent on where animals were located at the time of collection. While samples were collected throughout the park, the majority were concentrated in four locations of high species overlap including Hayden Valley, Lamar Valley, the area surrounding the North Entrance, and on the slopes of Mount Washburn. Sample collection in each location occurred over the duration of 1–6 days and spanned an area ranging between 1 and 10 km^2. In Hayden Valley and Lamar Valley, samples were collected from bison, elk, mule deer, and pronghorn. Samples were collected from each of the five studied species in the area surrounding the North Entrance. On Mount Washburn, samples were collected from bighorn sheep and mule deer. Samples were collected soon after elimination in order to ensure that they had not been contaminated by fungi, invertebrates, or microorganisms. Dried, homogenized samples (2–3 mg) were loaded into 5 X 8 mm tin capsules and analyzed for stable carbon isotope ratios using a Carlo Ebra elemental analyzer attached to a Micromass Europa Mass Spectrometer at the Centre for Stable Isotope Biogeochemistry at the University of California Berkeley. Nitrogen content of the samples was determined by gas chromatography prior to isotope analysis and is reported as percentage per sample to the nearest 0.1%. Carbon stable isotope values are reported in parts per thousand (‰) and were obtained using the following equation: $\delta^{13}C = 1000\ [R_{sample}/R_{standard}] - 1$, where R_{sample} and $R_{standard}$ are the ratio of $^{13}C/^{12}C$ of the sample and the standard. The standard used was the Vienna Pee Dee Belemnite (VPDB). Replicate measurements of internal laboratory standard NIST 1547 (peach leaves) indicated measurement precision was 0.1‰.

Data analysis

We used linear regression to evaluate the relationship between FN and body size, to test our prediction that diet quality would decrease with increasing body size. Body size for each species was calculated using the mean body mass reported for males and females (Table 1). Body mass was log-transformed to improve the fit of the linear model.

Table 1 Seasonal fecal nitrogen (FN) concentration of the YNP ungulate species

Species	Body mass (kg)	FN Summer 2002					FN 2003					FN Winter 2004				
		N	Mean	Min	Max	SD	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD
Pronghorn	$48^{a,b}$	16	1.92	1.24	2.91	0.45	30	2.20	1.46	3.01	0.31	15	1.49	1.25	1.92	0.20
Mule deer	$72^{g,h}$	9	2.46	0.92	3.50	0.70	8	3.34	2.43	4.43	0.60	11	1.62	1.31	1.98	0.21
Bighorn sheep	$78^{i,j}$	12	2.52	2.26	2.95	0.21	5	2.39	2.25	2.54	0.11	6	1.21	1.03	1.40	0.13
Elk	$270^{e,f}$	20	2.24	1.05	2.97	0.58	5	2.28	2.01	2.71	0.28	34	1.24	0.61	1.52	0.16
Bison	$617^{c,d}$	30	1.68	0.63	2.85	0.46	3	1.95	1.79	2.19	0.21	21	1.26	1.10	1.43	0.09

Sample size, body mass, mean, minimum, maximum, and standard deviation are reported

[a]Barnowe-Meyer and White (2017), [b]Mitchell (1980), [c]Berger and Peacock (1988), [d]Meagher (1986), [e]Urtin and Hobson (2005), [f]Cassier et al. (1992), [g]Bleich et al. (2003), [h]Hakonson and Whicker (1971), [i]Poissant et al. (2008), [j]Pelletier and Festa-Bianchet (2004)

We assessed interspecific differences in FN and δ^{13}C values using parametric (One-way ANOVA, Tukey's HSD) and nonparametric (Kruskal–Wallis) tests where appropriate. This was done to test our prediction that larger-bodied species would have significantly different diets from smaller-bodied species. Levene's test for homogeneity of variance was used to examine seasonal differences in intraspecific FN and δ^{13}C variation. We used linear regression to evaluate the relationship between FN, δ^{13}C, and elevation. Elevation was log-transformed to improve the fit of the linear model. All analyses were carried out in R 4.3.0 with significance set at $\alpha = 0.05$.

Table 2 Significant differences in δ^{13}C (top) and FN (bottom) shown in post hoc contrasts of species pairs

Species		Pronghorn	Bison	Elk	Mule deer
Summer 2002					
	Bison	**< 0.01**			
		0.51			
	Elk	**< 0.01**	0.08		
		0.32	**< 0.01**		
	Mule deer	**< 0.01**	**< 0.01**	0.55	
		0.08	**< 0.01**	0.80	
	Bighorn sheep	0.16	**0.03**	**< 0.01**	**< 0.01**
		0.02	**< 0.01**	0.52	0.99
Summer 2003					
	Bison	0.56			
		0.17			
	Elk	**< 0.01**	0.20		
		0.74	0.17		
	Mule deer	**< 0.01**	**0.18**	1.00	
		< 0.01	**< 0.01**	**< 0.01**	
	Bighorn sheep	0.98	0.50	**< 0.01**	**< 0.01**
		0.11	**0.03**	0.33	0.11
Winter 2004					
	Bison	**< 0.01**			
		0.508			
	Elk	**< 0.01**	0.87		
		< 0.01	0.53		
	Mule deer	**< 0.01**	0.92	0.82	
		0.29	**< 0.01**	**< 0.01**	
	Bighorn sheep	**0.01**	0.49	0.54	0.49
		< 0.01	**0.02**	0.85	**< 0.01**

Values shown in bold indicate significance for $\alpha = 0.05$

Results

Effect of body size on fecal nitrogen values

We found a negative association between FN and body mass across seasons (summer 2002, $R^2 = 0.12$; summer 2003, $R^2 = 0.04$; winter 2004, $R^2 = 0.25$) however, the model did not account for a significant proportion variation (Fig. 1). The association between FN and body mass was significant during the summer of 2002 and winter of 2004. While the effect of body mass on FN was consistently negative, it was most pronounced during the winter season (Fig. 1).

Interspecific differences in fecal nitrogen and carbon stable isotope values

We found significant differences in FN across species during each season (summers of 2002, $F_{4,82} = 9.53$, $p < 0.001$; summer 2003, $H_{4,\ 51} = 23.65$, $p < 0.001$; winter 2004, $H_{4,87} = 38.292$, $p < 0.001$). Post hoc contrasts revealed several significant differences between species pairs that align with differences in body mass (Table 2). In line with our prediction that larger-bodied species would have lower FN than smaller-bodied species, bison showed significantly

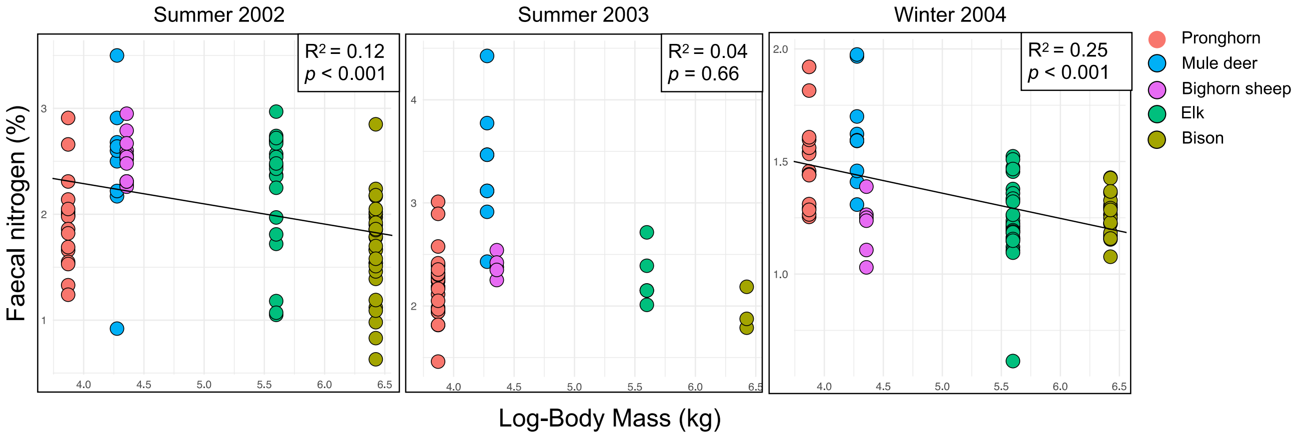

Fig. 1 Scaling of faecal nitrogen (FN) with body mass. Lines are linear regressions

lower FN than bighorn sheep, mule deer, and elk. We found that the two smallest-bodied species, pronghorn and mule deer, had significantly higher FN than all other species during the winter (Tables 1, 2). Counter to our prediction, bighorn sheep had significantly higher FN than smaller-bodied pronghorn during the summer of 2002. Further, we found that larger-bodied mule deer had significantly higher FN than pronghorn during the summer of 2003. There were a greater number of significant interspecific differences during the winter than the summer. All species showed a decrease in FN from summer to winter (Table 1, Fig. 2). The range of interspecific mean FN was greater during the summer (2002: 1.68–2.52%; 2003: 1.95–3.34%) than the winter (1.21–1.62%).

δ^{13}C also differed significantly across species during each season (summer 2002, $F_{4,82} = 23.73$, $p < 0.001$; summer 2003, $F_{4,46} = 15.01$, $p < 0.001$; winter 2004, $F_{4,82} = 16.86$, $p < 0.001$). Post hoc contrasts showed several significant differences between species pairs; however, these differences did not align discernibly with body mass (Table 2). Pronghorn consistently had higher δ^{13}C values than larger-bodied species (Tables 2, 3). Bison had the lowest δ^{13}C values during the winter of 2004. We found a greater number of significant interspecific differences in δ^{13}C during the summers than the winter. All species showed an increase in δ^{13}C values from summer to winter (Fig. 3). The range of interspecific mean δ^{13}C was greater during the winter (−25.15 to −27.16‰) than the summer (2002: −27.24 to −28.41‰; 2003: −27.56 to −28.94‰).

Intraspecific variation in fecal nitrogen and carbon stable isotope values

We found that differences in the breadth of intraspecific FN variation rarely aligned with body mass (Table 1, Fig. 2). This finding runs counter to our prediction that smaller-bodied species would have narrower dietary breadth than larger-bodied species. In line with our prediction, bighorn sheep showed the lowest range of FN variation during both summer seasons. However, similarly sized mule deer showed the greatest range during both summer and winter (Fig. 2). Further, bison showed the lowest range of variation during the winter. Across species we found that the range of FN variation decreased from summer to winter. We found no significant difference in the range FN variation for any species between the two summer seasons. However, there was a significant difference for most species between summer and winter (Table 4).

Mirroring the results for FN, differences in the range of intraspecific δ^{13}C variation infrequently aligned with body mass (Table 3, Fig. 3). While bighorn sheep had the lowest range of variation during the summer of 2003 and winter of 2004, mule deer showed the greatest range of variation during the same two seasons. Further, bison had the narrowest range of variation during the summer of 2002. Across species we found that the range of δ^{13}C variation decreased from summer to winter. All species except pronghorn had a similar range of variation during the two summer seasons. In contrast, elk, mule deer, pronghorn, and bison showed

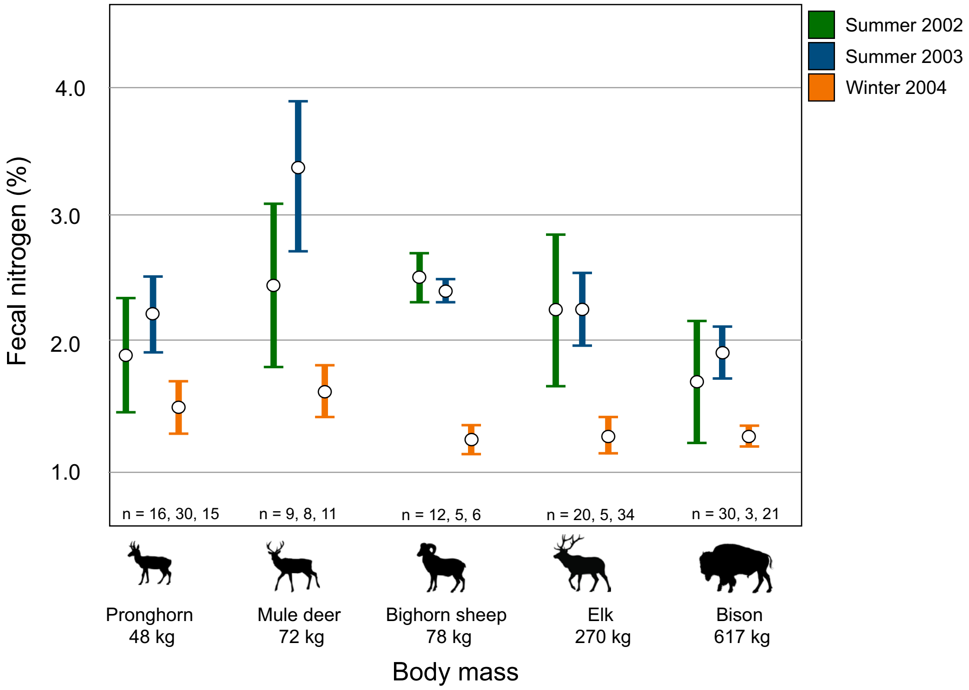

Fig. 2 Mean ± standard deviation plots of fecal nitrogen (FN) for the Yellowstone National Park (YNP) ungulate species. Body mass is shown along the x-axis. Mammal reconstructions are not to scale. Associated post hoc statistics found in Table 1

Table 3 Seasonal $\delta^{13}C$ values of the YNP ungulate species

Species	Body mass (kg)	$\delta^{13}C$ Summer 2002					$\delta^{13}C$ 2003					$\delta^{13}C$ Winter 2004				
		N	Mean	Min	Max	SD	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD
Pronghorn	48	16	−27.24	−27.58	−26.43	0.27	30	−27.69	−28.36	−26.47	0.51	15	−25.15	−26.94	−23.42	1.16
Mule deer	72	9	−28.41	−29.15	−27.62	0.50	8	−28.90	−29.57	−27.72	0.60	11	−26.87	−28.22	−24.92	1.24
Bighorn sheep	78	12	−27.55	−27.90	−27.22	0.22	5	−27.56	−27.80	−27.27	0.20	6	−27.04	−27.20	−26.81	0.18
Elk	270	20	−28.19	−28.97	−26.87	0.56	5	−28.94	−29.34	−28.42	0.44	34	−27.10	−28.31	−25.40	0.71
Bison	617	30	−27.92	−28.49	−27.56	0.20	3	−28.14	−28.44	−27.76	0.35	21	−27.16	−27.85	−25.70	0.54

Sample size, body mass, mean, minimum, maximum, and standard deviation are reported

significant differences in their range of variation between the summer and winter (Table 5).

Effect of elevation on fecal nitrogen and carbon stable isotope values

We found a positive association between FN and elevation during summers (summer 2002, $R^2=0.04$; summer 2003, $R^2=0.06$) and a negative association during winter ($R^2=0.08$), however, the model did not account for a significant portion of variation (Fig. 4). The association between FN and elevation was significant during the winter, but non-significant during the summers. We found a negative association between $\delta^{13}C$ and elevation throughout each season (summer 2002, $R^2=0.06$; summer 2003, $R^2=0.01$; winter 2004, $R^2=0.05$) (Fig. 5), but again, the model did not account for a significant portion of variation. The association between $\delta^{13}C$ and elevation was significant during the summer of 2002 and winter of 2004, but non-significant during the summer of 2003.

Discussion

Evaluating the factors that act to reduce interspecific competition among ecologically similar species is key to understanding the assembly and evolution of herbivore communities. The JBP represents a major organizing concept in large herbivore ecology and asserts that larger-bodied species will consume greater amounts of relatively low-quality forage, whereas smaller-bodied species selectively consume higher quality diets (Bell 1971; Jarman 1974). In this study we examined the influence of body size on diet quality and breadth in the ungulate community in YNP. Our aim was to assess the applicability of the JBP in a temperate C_3-dominant North American ecosystem. With some exceptions, the results support the JBP in showing that diet quality, as indicated by digestibility, declined significantly with body size. The results do not, however, support the prediction that body size would influence dietary breadth.

During two out of three seasons we found a significant negative relationship between FN and body mass (Fig. 1), indicating that the mean digestibility of diet declined with increasing body mass. This finding is congruent with the core empirical prediction of the JBP: a negative correlation between diet quality and body size in free-ranging herbivores. However, the strength of the relationship between body mass and diet quality in the sampled YNP ungulates was strongly influenced by outliers. This issue is exemplified when considering the expansive range of variation in FN displayed by mule deer. Often characterized as a highly opportunistic browser, this cervid is known to consume a range of resource types of varying digestibility including

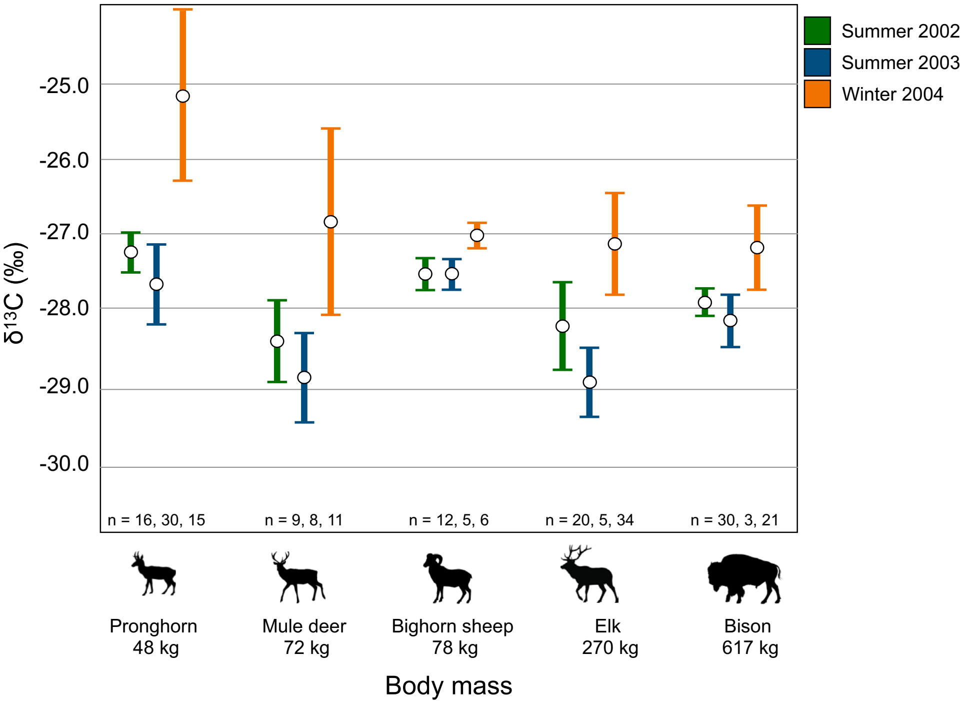

Fig. 3 Mean ± standard deviation plots of carbon stable isotope values ($\delta^{13}C$) for the Yellowstone National Park (YNP) ungulate species. Body mass is shown along the x-axis. Mammal reconstructions are not to scale. Associated post hoc statistics found in Table 3

Table 4 Seasonal comparison of intraspecific FN variation

Species	Summer 2002 versus Summer 2003			Summer 2002 versus Winter 2004			Summer 2003 versus Winter 2004		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
Pronghorn	2.55	44	0.12	5.37	29	**0.03**	1.25	43	0.27
Mule deer	0.01	15	0.94	4.08	18	0.06	6.36	17	**0.02**
Bighorn sheep	2.02	15	0.18	1.33	16	0.27	0.28	9	0.61
Elk	0.01	23	0.98	31.37	52	**< 0.01**	26.23	37	**0.01**
Bison	1.28	31	0.27	18.5	49	**< 0.01**	5.82	22	**0.03**

p-values shown in bold indicate significance for alpha = 0.05

Table 5 Seasonal comparison of intraspecific $\delta^{13}C$ variation

Species	Summer 2002 versus Summer 2003			Summer 2002 versus Winter 2004			Summer 2003 versus Winter 2004		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
Pronghorn	17.29	44	**< 0.01**	45.2	29	**< 0.01**	32.19	43	**< 0.01**
Mule deer	0.31	15	0.59	7.98	18	**0.01**	5.3	17	**0.03**
Bighorn sheep	0.22	15	0.64	0.16	16	0.69	0.025	9	0.88
Elk	0.07	23	0.80	2.19	52	0.15	1.25	37	0.27
Bison	1.89	31	0.18	13.7	49	**< 0.01**	0.52	22	0.48

p-values shown in bold indicate significance for alpha = 0.05

forbs, shrubs, sedges, fungus, and fruit (Deschamp et al. 1979; Singer and Norland 1994; Stewart et al. 2003). Further confounding the relationship between body size and diet quality was our finding that certain species would follow the predicted pattern during one season, but not the other. For example, pronghorn had significantly higher FN than many large-bodied species during the winter but had significantly lower FN than larger-bodied bighorn sheep and mule deer during both summers. The noisy association between body mass and diet quality that we observed in YNP is characteristic of empirical studies of the JBP (Garnick et al. 2018; Potter et al. 2022; Daskin et al. 2023). Of the various

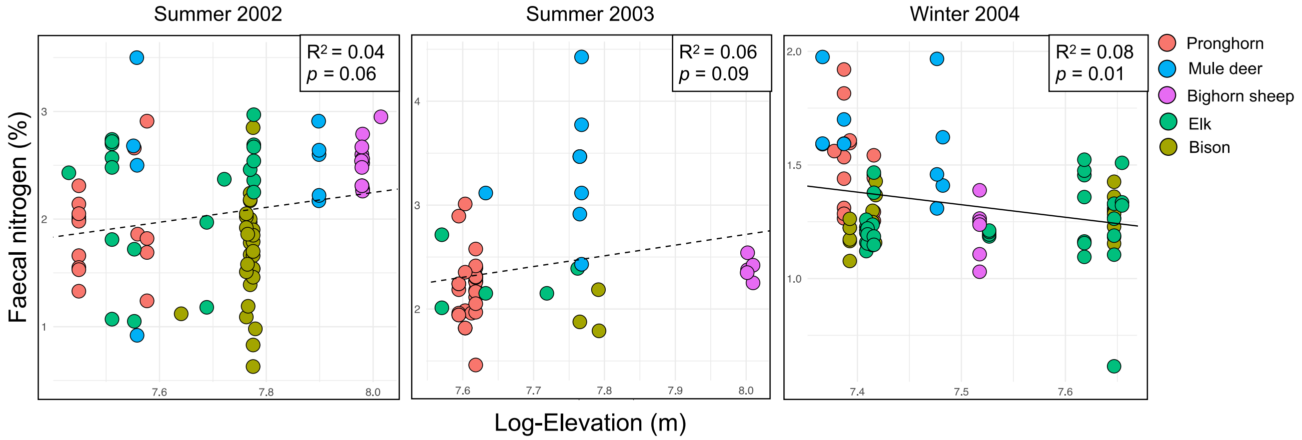

Fig. 4 Association between FN values and elevation. Lines are linear regressions

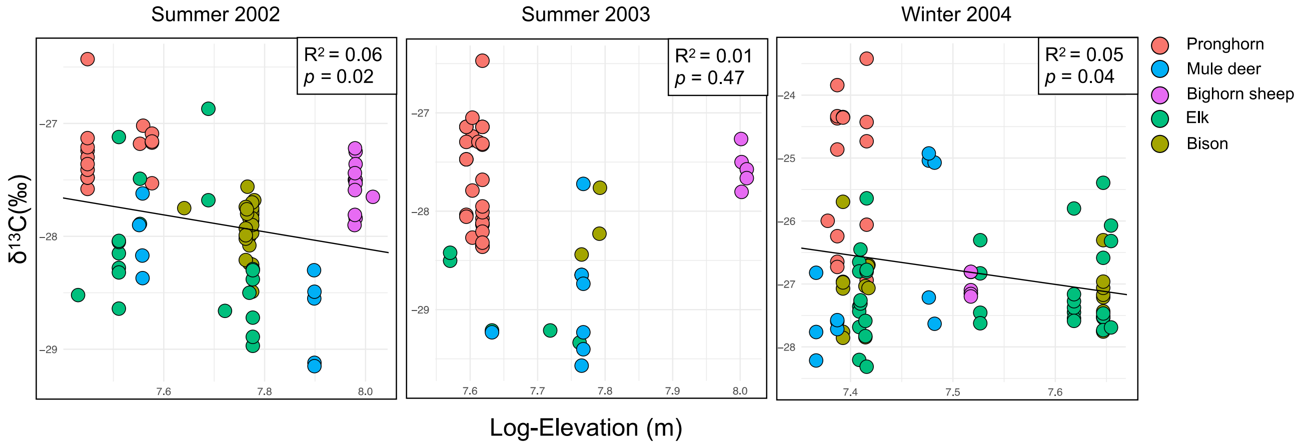

Fig. 5 Association between carbon stable isotope values ($\delta^{13}C$) and elevation. Lines are linear regressions

mechanisms suggested to explain the JBP, the ecological trade-off hypothesis best accommodates the noise and outliers commonly reported. This hypothesis posits that while all herbivores must navigate a diet quantity-quality trade-off, larger herbivores should generally sacrifice quality to a greater extent than smaller herbivores because of their larger absolute nutritional requirements, and because their big bodies make it harder to harvest large amounts of high-quality plants. Species-specific traits and environmental attributes act to modulate the tendency of these factors to promote a negative body size-diet quality relationship (Potter and Pringle 2023).

We found that the negative relationship between diet quality and body mass was stronger during the winter when preferred plant resources became scarce. There were a greater number of significant interspecific differences in FN during the winter, suggesting an increased level of dietary niche segregation. Further, we found an increase in the range of interspecific mean $\delta^{13}C$ values during winter, which indicates more pronounced differences in the plants or plant parts consumed by each species. This pattern of increased dietary niche segregation during the lean season is common across taxa and has been interpreted as interspecific competition operating on multiple scales (Schoener 1982; Gordon and Illius 1989). During periods of resource scarcity, selection favours traits that enable species to use certain foods more efficiently than their competitors, and it is those specific foods that each species will focus their foraging efforts upon. Pansu et al. (2022) report similar findings from their fecal DNA metabarcoding analysis of large herbivore diet in southeastern Africa. These authors found that food plant partitioning was stronger between species of different body size and that the strength of plant partitioning was greater during the dry season when resources were scarce. The mirroring of this pattern in our study of a temperate North American ecosystem lends support to the generalizability of the JBP. Nonetheless, caution is critical when considering the broadscale applicability of this hypothesis, as highlighted by a recent study of mega- and meso-herbivores in Assam, northeastern India, which found that body size did not explain interspecific differences in diet (Devi et al. 2022).

Although the results do support a negative allometric relationship between body mass and diet quality, we found little evidence suggesting that body mass influenced dietary breadth. We predicted that selective feeding by smaller-bodied herbivores on higher-quality foods would lead to a narrower range of FN and $\delta^{13}C$ values; however, this was not the case for most of the YNP ungulates. In fact, we found that the two species most similar in body mass, bighorn sheep and mule deer, collectively displayed both the narrowest and broadest range of variation in FN and $\delta^{13}C$ values. The lack of association between body mass and dietary breadth observed here accords with the findings of several recent studies (Kartzinel et al. 2015; Kartzinel and Pringle 2020; Hutchinson et al. 2022; Daskin et al. 2023). Kartzinel and Pringle (2020) examined the relationship between taxonomic and phylogenetic dietary diversity among large mammalian herbivores in a semi-arid East African savanna and found that body mass did not predict dietary diversity.

Seasonal differences in the range of intraspecific FN and $\delta^{13}C$ variation generally followed predicted environmental patterns. FN variation decreased across species from summer to winter, which accords with the seasonal decrease in protein and favourable mineral concentration of forage plants in temperate environments. The content of hemicellulose in forbs and shrubs generally increases with maturity and the cellulose content of graminoids can increase by up to 50% from summer to winter (Moser et al. 2006). Our findings are congruent with general seasonal trends observed in other wild ungulate species (Verheyden et al. 2011; Gálvez-Cerón et al. 2013; Ramanzin et al. 2017; Espunyes et al. 2022), reflecting an increase in diet quality during the spring/summer and decline in fall/winter. Similarly, the observed increase in $\delta^{13}C$ values from summer to winter is concordant with studies in other temperate C_3-dominant ecosystems (Metclafe 2021). Metcalfe (2021) examined plant isotopic variability in a boreal mixed woodland ecosystem in Alberta, Canada, and found a 1‰ increase in $\delta^{13}C$ from summer to fall. This author attributes the increase in $\delta^{13}C$ to a combination of factors including changes in the biochemical compositions of plant tissues, changes in source carbon isotopic compositions, remobilization of nutrients into roots for winter, and early decomposition. Seasonal changes in the diets of a range of large herbivores living in temperate C_3-dominant ecosystems have been studied, and variation in $\delta^{13}C$ values are typically relatively small in magnitude (~2 to 3‰ or less; Keilland 2001; Julien et al. 2012; Funck et al. 2020), which accords with our finding of a 1 to 2‰ seasonal difference in the $\delta^{13}C$ values of the YNP ungulates.

Notwithstanding the low levels of intra- and interspecific variation in $\delta^{13}C$, the results do show significant differences between species that accord with observed variations in habitat use within the park. During both summer seasons, mule deer and elk displayed significantly lower $\delta^{13}C$ than the other sampled species, which is consistent with a habitat preference for wet meadows and coniferous forests. These species share an overlapping annual range and utilize many of same movement corridors within the park (White et al. 2010; Gogan et al. 2019). In contrast, bighorn sheep, bison, and pronghorn shared similarly higher $\delta^{13}C$ during the summers, which accords with a more open habitat preference. Bison and pronghorn are associated with grassland and shrub-steppe habitats, and bighorn sheep are typically found in open and rocky alpine and subalpine areas (Singer and Norland 1994; Yoakum 2004). During winter only pronghorn differed significantly from the other sampled species, limiting interpretations of differential habitat use. Pronghorn had significantly higher mean $\delta^{13}C$ than all other species, which is congruous with overwintering in open low-elevation, windswept areas where snow is less deep and allows for selective foraging on sagebrush (Singer and Norland 1994; Yoakum 2004; Boccadori et al. 2008; Barnowe-Meyer et al. 2017). We found a negative association between $\delta^{13}C$ and elevation during each season (Fig. 5). This was unexpected and differs from the positive correlation previously reported for livestock (Männel et al. 2007). Our findings are congruent with the results of several plant studies conducted in alpine regions of northern Spain (Tornero et al. 2018), central China (Liu et al. 2016), and Mongolia (Makarewicz and Tuross 2006). Notably, the negative pattern reported here accords with a recent study of ungulate tissues in the Mongolian Altai that showed a significant negative correlation between $\delta^{13}C$ and grazing altitude (Lazzerini et al. 2021). Our results add to the growing body of research demonstrating an association between variations in plant and animal $\delta^{13}C$ values and elevation. The specific factors influencing this relationship are thought to be site specific, with several authors proposing that local climatic factors influence water availability and thereby complicate the relationship between plant $\delta^{13}C$ and elevation (Morecroft and Woodward 1990; Liu et al. 2007, 2010).

We found seasonal differences in the association between FN and elevation that generally follow patterns observed in other temperate migratory ungulates (Festa-Bianchet 1988; Albon and Langvatn 1992; Sakuragi et al. 2003). There was a positive but non-significant association between FN and elevation during the summers, and a significant negative association during the winter (Fig. 4). These findings are congruent with the idea that protein content and digestibility of plants are correlated with elevation (Van Soest 1983), and that FN can be used to track seasonal changes in foraging elevation (Festa-Bianchet 1988; Albon and Langvatn 1992;

Sakuragi et al. 2003). We found interspecific differences in FN that support these interpretations, with bighorn sheep, the only studied species consistently associated with higher elevation habitats, showing significantly higher summer FN than pronghorn (Fig. 4). Similarly, mule deer, which were sampled from a range of higher and lower elevation habitats, also had significantly higher summer FN than pronghorn. These findings run counter to predictions based on body size and suggest that foraging elevation also influenced diet quality. Similar results were reported in a study of migratory Sika deer (*Cervus nippon*) in eastern Hokkaido, where authors found a significant positive correlation between the summer FN and elevation, indicating that individuals foraging at higher elevations gained access to better quality diets (Sakuragi et al. 2003). During winter the association between FN and elevation was negative, indicating a decrease in diet quality with increasing elevation. This accords with diminished winter plant growth at higher elevations, where snow cover lasts longer and temperatures are lower resulting in decreased access to high protein and low fibre forage (Klein 1970; Langvatn and Albon 1986; Albon and Langvatn 1992; Sakuragi et al. 2003). Each of the studied species were sampled at lower elevations during winter, including bighorn sheep, which seasonally descend from their alpine habitats to overwinter in lower elevation areas of the park. During winter the FN of bighorn sheep was significantly lower than pronghorn and mule deer, following the empirical pattern predicted by the JBP (Fig. 4). While the current study was not explicitly designed to assess spatial differences in diet quality, our results highlight the challenge of differentiating between several non-mutually exclusive factors influencing diet quality in wild ungulates.

In this study we used FN as an indicator of diet quality linked to overall digestibility. It is prudent to again outline factors that have been shown to limit the utility of FN as an indicator of diet quality, and thus temper our interpretations with caution. The relationship between FN and diet quality can be obscured if animals feed on plants rich in secondary compounds, such as tannins, because tannins may inhibit the digestion of protein and fibre which are excreted as non-metabolic nitrogen (Frutos et al. 2004), thus reducing the amount of digestible protein in forage and increasing FN (Kariuki and Norton 2008). This effect has been shown repeatedly in free-ranging herbivores (Leslie et al. 2008; Verheyden et al. 2011; Caprio et al. 2015). We acknowledge that the influence of tannins could have resulted in elevated FN in both mule deer and elk, as both species are known to seasonally consume plants and plant parts that can be high in tannins (Deschamp et al. 1979; Singer and Norland 1994). However, even if mule deer and elk are excluded from consideration, the negative association between body size and diet quality remains amongst the other YNP ungulates. Interspecific differences in FN between bison, bighorn sheep, and pronghorn generally follow differences body size. Another cause for caution in the interpretation of FN was recently highlighted in an environmentally controlled study of red deer (*Cervus elaphus*). Čupić et al. (2021) showed that differences in factors such as age, body mass, sex, reproductive status, and body condition were associated with high levels of variation in FN. Because these factors cannot always be readily assessed when studying free-ranging ungulates, interpretations of FN as a measure of diet quality can be misleading. While we did generally control for age by collecting samples from adults, we did not assess specific body mass, sex, reproductive status, or body condition. Finally, we note that while FN and δ^{13}C can provide important information about the plant types and even plant parts consumed by herbivores, neither proxy affords the determination of taxonomic identity. Without this level of resolution, we are unable to assess cryptic niche differences and the degree to which individual specialization is acting to increase the populations dietary niche breadth. With this in mind, we suggest that future research examining trophic niche dynamics among the YNP ungulates include fecal DNA metabarcoding. This method of analysis has proven highly effective for elucidating finite dietary differences and untangling the various factors influencing dietary niche differentiation (Kartzinel and Pringle 2020; Devi et al. 2022; Hutchinson et al. 2022; Pansu et al. 2022; Potter et al. 2022; Walker et al. 2023; Daskin et al. 2023).

Conclusions

Investigating the factors that promote coexistence between ecologically similar species is key to understanding community diversity and function. The JBP presents a trade-off between diet quality and quantity as an axis for dietary niche segregation and has often been put forth as a mechanism facilitating species coexistence (Jarman and Sinclair 1979; Kleyhans et al. 2011; Owen-Smith et al. 2017). Our study used FN and δ^{13}C values to evaluate the influence of body size on patterns of dietary niche segregation within the ungulate community in Yellowstone National Park. We specifically tested the influence of body mass on diet quality and breadth. The results generally follow the empirical pattern predicted by the JBP in showing that diet quality, as indicated by digestibility, declined significantly with increasing body mass. We found that the relationship between diet quality and body mass was more pronounced during the winter when resources were scarce. There were also a greater number of significant interspecific differences in diet quality during the winter. These findings accord with the interpretation that periods of resource scarcity favour the selection of traits that enable species to use certain foods more efficiently than their competitors.

We found little evidence indicating that dietary breadth scaled with body mass. In fact, the two species most similar in body mass displayed the greatest and least range of variation in both FN and $\delta^{13}C$ values. Seasonal differences in the range of intraspecific FN and $\delta^{13}C$ variation generally followed predicted environmental patterns. We found a positive relationship between diet quality and elevation during the summer and a negative relationship during winter. These findings accord with previous studies of migratory ungulates in temperate environments. While interspecific differences in $\delta^{13}C$ were relatively small in magnitude, significant differences between species are in line with observed variations in habitat use. Identifying significant, albeit noisy, empirical support for the JBP in a temperate North American ecosystem serves to extend the environmental and taxonomic generalizability of one of the most important organizing principles in large herbivore ecology. Our results underscore the importance of body size as a factor facilitating dietary niche segregation and promoting coexistence among ecologically similar ungulate species.

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Author contributions LCE developed study, RSF conducted fieldwork and collected data, LCE analyzed data and wrote manuscript with editorial input from RSF.

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Code availability Not applicable.

Declarations

Conflict of interest All authors declare that they have no conflict of interest.

Consent to participate Not applicable.

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Ethics approval Not applicable.

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