ORIGINAL ARTICLE

Food patch selection by the largest European herbivore

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Abstract

The scaling relationship between digestive system and body mass shapes foraging strategies in herbivores. The Jarman–Bell principle and the forage maturation hypothesis (FMH), two of the most important predictions formulated in herbivore foraging ecology, have been used to explain this relationship.We aimed to test these predictions for the largest European herbivore—the European bison-which is highly sexually dimorphic and recognised as a refugee species in non-optimal forest habitats. We conducted our study in the Białowieża Primeval Forest, where the European bison has been recognized as a refugee species. We estimated vegetation quality and biomass along the foraging paths of male and female European bison, and the vegetation biomass at random points in different habitats and months. We found no support for the Jarmann-Bell principle at the intraspecific level in European bison, as males and females foraged on patches of similar crude protein and fibre content. However, females selected for higher biomass. The quality of vegetation on the bison foraging patches showed a significant spatio-temporal variation. It increased from May to July and then gradually decreased. It also increased with the fertility and wetness of the habitats being the highest in wet forests. Mean biomass on European bison foraging patches (131.5 g/m^2), was significantly lower than on random plots (210.5 g/m^2), which supported the FMH. Our study suggests that in rich forest habitats, the abundant food resources available in summer may not constrain the metabolic rate/gut capacity ratio of either sex, potentially leading to dietary segregation. In contrast to open habitats, where vegetation maturation is less temporally variable, European bison in rich forest habitats may optimise patch selection and energy intake by tracking a habitat- and species-specific changes in the plant phenology. Understanding the relationship between European bison forage selection and forage nutritional constraints in forest habitats may be critical for conservation programmes, as European bison are better adapted to more open habitats and are recognised as refugee species in suboptimal forest habitats.

Keywords European bison · Foraging ecology · Forage quality · Forage maturation hypothesis · Jarman-Bell principle · Sexual dimorphism

Introduction

The relationships between body size and digestive system shape resource selection by ungulates and are fundamental for understanding foraging strategies of herbivores (Esmaeili et al. 2021). It is widely accepted that large-bodied species can or must ingest diets of lower quality because of their lower metabolism requirement/gut capacity ratio (Demment and Van Soest 1985). This prediction was formulated as a Jarman–Bell principle (Bell 1970, 1971; Jarman 1974; Geist 1974) and it was mainly tested on inter-specific level (Owen-Smith 1988; Codron et al. 2007; Pérez-Barbería et al. 2008). However, Jarmann–Bell principle should also apply to intra-specific interactions for ungulate species that exhibit pronounced sexual body size dimorphism (Pérez-Barbería et al. 2008). Females, due to their smaller size and related lower rumen capacity, have faster food-passage rate than males and thereby require forage of higher quality (Berini and Badgley 2017). Females also have higher energy requirements due to pregnancy and lactation. During the last trimester of pregnancy, these costs are almost 50% higher than for non-pregnant individuals, while during the first months post partum, requirements increase by 65–215% for ungulate females (Parker et al. 2009; Pekins et al. 1998; Robbins 1993).

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Limited studies on intra-specific variation in diet quality in ungulates do not clearly demonstrate that Jarmann-Bell principle applies also at species level (Gross et al. 1996; Pérez-Barbería et al. 2008). Sex-specific differences in diet quality were confirmed for American bison (Berini and Badgley 2017). Studies on two Caprine species showed that differences in the efficiency of food digestion associated with body mass were not due to differences in food selection, but probably they were related to more efficient comminution of the forage by females (Gross et al. 1996; Pérez-Barbería et al. 2008).

Body size creates also trade-offs in how ungulates should balance forage biomass and it's digestibility (Bailey et al. 1996; Olff et al. 1999; Wilmshurst et al. 2000). Increasing biomass and maturation of vegetation decrease nutritive value and digestibility of forage, which is related mainly to increasing fiber content in plants (Belovsky 1978; McNaughton 1985; Van Soest 1994). Because of this trade-offs, the energy intake should be at maximum when the rates of both forage intake and digestibility are at intermediate levels (Esmaeili et al. 2021) what constitutes the main assumption of the forage maturation hypothesis (FMH) (McNaughton 1984, Fryxell 1991). FMH has been recently confirmed by the models of patch selection by herbivores (Raynor et al. 2016), however it was most frequent among smaller-bodied ungulates (Esmaeili et al. 2021). This indicates that selecting forage at early to intermediate phenological stages reflects rather the higher mass-specific energetic requirements of smaller ungulates (Hopcraft et al. 2012; Illius and Gordon 1987).

Majority of megaherbivores in Europe got extinct before the Pleistocene/Holocene transition (Cooper et al. 2015; Stuart 2015). One of the very few survivors of this guild is European bison—the largest terrestrial mammal of Europe. The species was recognized as well-adapted to open habitats (Mendoza and Palmqvist 2008; Bocherens et al. 2015), that due to forest expansion and increasing human pressure during the Holocene became refugee species in forest habitats (Kerley et al. 2012). Further deforestations and hunting pressure caused declining densities and fitness, that led to progressive disappearance of European bison from the continent (Kerley et al. 2012; Hofman-Kamińska et al. 2019; Pilowsky et al. 2023). The species was extirpated in the wild at the beginning of twentieth century and restored from captive survivors (Pucek et al. 2004; Tokarska et al. 2011). The process started in Białowieża Primeval Forest (BPF), and after successful release of European bison into the wild in 1950s, it has been continuously re-introduced or introduced in Eastern Europe, mainly to forested areas. Nowadays European bison occurs in nearly 50 locations. Consequently, bison population size has been constantly increasing (Plumb et al. 2020; Kowalczyk and Plumb 2022).

European bison expresses apparent sexual body size dimorphism, with males (mean body mass 630 kg) being on average 50% heavier than females (mean body mass 424 kg) (Krasińska and Krasiński 2002). During growing season bison males are solitary (62% of males) or form small bachelor groups (up to 8 individuals), while females with calves and sub-adults roam in mixed groups (11–15 individuals, on average) (Krasińska and Krasiński 1995; Krasińska et al. 2000). Herd size increases during the rutting season (August–October) and in winter when bison often create large aggregations. In forest habitats, the species was recognised as a browser or mixed feeder (Kowalczyk et al. 2011, 2019; Merceron et al. 2014; Hartvig et al. 2021). The survival of European bison after Holocene environmental changes and their persistence in suboptimal forest habitats as results of increasing human pressure may indicate a high degree of foraging plasticity in the species (Kowalczyk et al. 2011, 2019; Hofman-Kamińska et al. 2019).

One of the characteristics of forest communities is the patchiness of plant distribution (Bobiec 1998). This patchiness is influenced by various factors, including plant life strategies, soil diversity and water regimes, microclimatic variables, habitat and stand heterogeneity, age structure and gap dynamics, forest management and protection (e.g. Bobiec 1998; Corney et al. 2006; Bähner et al. 2020; Czerepko et al. 2021). This creates a mosaic of food patches that differ in plant biomass, digestibility and species composition, to which ungulates may respond through foraging behaviour to optimise energy intake (Ramirez et al. 2023).

In this paper we aimed to investigate the selection of food patches by the largest and sexually dimorphic European herbivore in forest habitats. Specifically, we tested the Jarman–Bell principle and the food maturation hypothesis. We hypothesized that a large sex-specific difference in bison body size and gut capacity would result in niche segregation and feeding on patches differing in forage quality by males and females. We predicted that male forage would be of lower quality than female. Furthermore, we expected that bison would optimize nutrient intake by selecting patches of low to intermediate vegetation biomass.

Materials and methods

Study area

The study was carried out in Białowieża Primeval Forest (BPF) in NE Poland (52°35′–52°55′N, 23°30′–24°00′E), encompassing 635 km^2 of lowland forests. It is one of the best preserved forest ecosystems in Europe with over 20 species of trees and more than 1,000 species of vascular plants. It is covered by a mosaic of different habitats including: coniferous forests (mainly Scots pine *Pinus silvestris*,

and Norway spruce *Picea abies*)—6.1% of the area, mixed forests (MF) (with Scots pine, Norway spruce, pedunculate oak *Quercus robur*, with admixtures of European hornbeam *Carpinus betulus*, birch *Betula* spp., and aspen *Populus tremula*)—39.4% of the area, deciduous forests (DF) (with oak, hornbeam, small-leaved lime *Tilia cordata*, and maple *Acer platanoides*)—34.9%, and wet forests (WF) (mainly black alder *Alnus glutinosa* and European ash *Fraxinus excelsior*)—12.6% (Sokołowski 2006). Open habitats within the forest including river valleys, meadows, and glades with settlements (M) covers 7.0% of the area. The biomass and species composition of herbaceous vegetation strongly varies between habitats, tree stands and seasons (Faliński 1986; Bobiec 1998; Kowalczyk et al. 2019). We studied the foraging behaviour of European bison in four habitat types: MF, DF, WF and M. Coniferous forests were not included in the analysis due to their low proportion in tree stands and infrequent use by bison.

The climate of the BPF is transitional between Atlantic and continental types with clearly marked seasons. The mean annual temperature is 6.9 °C, and average precipitation is 625 mm (Boczoń et al. 2018).

The BPF is inhabited by a natural community of central European ungulates, with red deer (*Cervus elaphus*) being the most abundant, followed by wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), European bison (*Bison bonasus*), and moose (*Alces alces*) (Bubnicki et al. 2019). The relatively low density of ungulates in BPF, compared to other studies (Kuijper et al. 2010), allows for shared use of the rich food resources without competitive interactions (Merceron et al. 2014; Kowalczyk et al. 2021). During the study European bison population numbered 451 individuals (16% of wild-living bison in Europe) (Raczyński 2009). In winter bison are supplementary fed to mitigate migrations outside the forest to farmland and human settlements and provide bison with forage which is limited at this part of the year in the forest habitats. However, an increasing number of European bison do not utilize winter supplementary feeding and seasonally migrate to open habitats (Hofman-Kamińska and Kowalczyk 2012; Kowalczyk et al. 2013). During the growing season, European bison display natural feeding behavior, foraging in forest habitats, mid-forest meadows and river valleys (Kowalczyk et al. 2019, 2021).

Data collection

Between May and September 2009, we collected herbaceous plant samples and measured plant biomass on European bison foraging paths in different habitats. To find out foraging bison, we localized VHF- and GPS-collared individuals in the forest. Occasionally, after visual sex identification, we collected plant samples from non-collared individuals. In all cases, bison were observed from the distance, and the sampling started once they left the patch. Males usually foraged solitary in small bachelor groups (2–4 individuals), while females in larger mixed groups, including females with calves and subadults (usually 10–20 individuals). In case of mixed groups we selected feeding paths of adult females on the basis of observation or size of hoofprints. Bison feeding paths were clearly visible in the forest floor vegetation (grazed vegetation, hoofprints).

Ungrazed plant biomass in the immediate vicinity (max. 0.5 m) of European bison feeding paths was measured with the disc meter (Bransby et al. 1977; Rayburn and Lozier 2003). It consists of a plexiglass plate (45×45 cm) which slides along a graduated measurement scale and relates actual biomass to the height resistance of the vegetation. Height of the aboveground biomass was measured when vegetation canopy stopped further falling of the plate. The vegetation covered by plate (0.2 m^2) of the disc meter was clipped and, then, after drying, the vegetation mass was correlated with vegetation height estimated with the disc meter (for details see Kowalczyk et al. 2019) ($R^2 = 0.74$, $P < 0.001$)). Finally, correlation parameters were used in a predictive equation ($y = 3.108x - 0.899$), assessing plant biomass on the basis of biomass height. In total, we collected 109 vegetation samples on bison paths: 76 from 21 collared individuals or herds with collared individuals, and 33 from non-collared individuals or herds.

Additionally, plant biomass was measured between May and September 2009 on 42 random plots distributed over studied habitats. On each plot, vegetation height was measured with a disc-meter on 4 randomly selected points within a radius of 20 m from the centre of the plot. A total of 1005 measurements were taken. Vegetation biomass was calculated using the prediction equation (see above).

Chemical analysis of plant samples

Samples of plant biomass collected on European bison foraging paths were dried in a drier at 55 °C to constant weight, weighed and chemically analysed in the laboratory of the University of Agriculture, Kraków, Poland. Crude protein (CP) was analysed by the Kjeldahl method (AOAC 1980) using a Kjeltec 2200 analyser (Foss). Fibre fractions (ADF, ADL, NDF) were determined according to the method of Goering and Van Soest (1970) using an Ankom 2000 automatic fibre analyser. In further analyses, CP and ADF were used as proxies for vegetation quality on European bison foraging patches.

Statistical analysis

Sex-specific differences in CP and ADF content of plants collected on European bison paths were tested with generalised linear models with a Gaussian error structure (link

"identity") (GLM1 and GLM2). In GLM1 the response variable was the percentage of CP in the forage, while in GLM2 it was the percentage of ADF. In both models, besides sex, habitat type (MF, DF, WF and M), and plant biomass were included as explanatory variables. In addition, we fitted month as quadratic polynomial. We compared the differences in plant biomass during the growing season between bison foraging patches and random sites using the generalized linear model with a gamma error structure (link "log") (GLM3). We used plant biomass as the dependent variable, while the explanatory part consisted of an interaction between month (quadratic polynomial) and biomass type (bison forage vs random sites). In all GLMs the month variable was standardized to a mean of 0 and an SD of 1. We found acceptable collinearity between explanatory variables (Generalized Variance Inflation Index < 1.35). For all GLMs we checked model assumptions by a visual inspection of diagnostic plots (residuals vs fitted values and Q-Q residuals). As model residuals were not heteroscedastic and normally distributed, we assumed that the model assumptions were met. All statistical analyses were performed in the program R (R Core Team 2024).
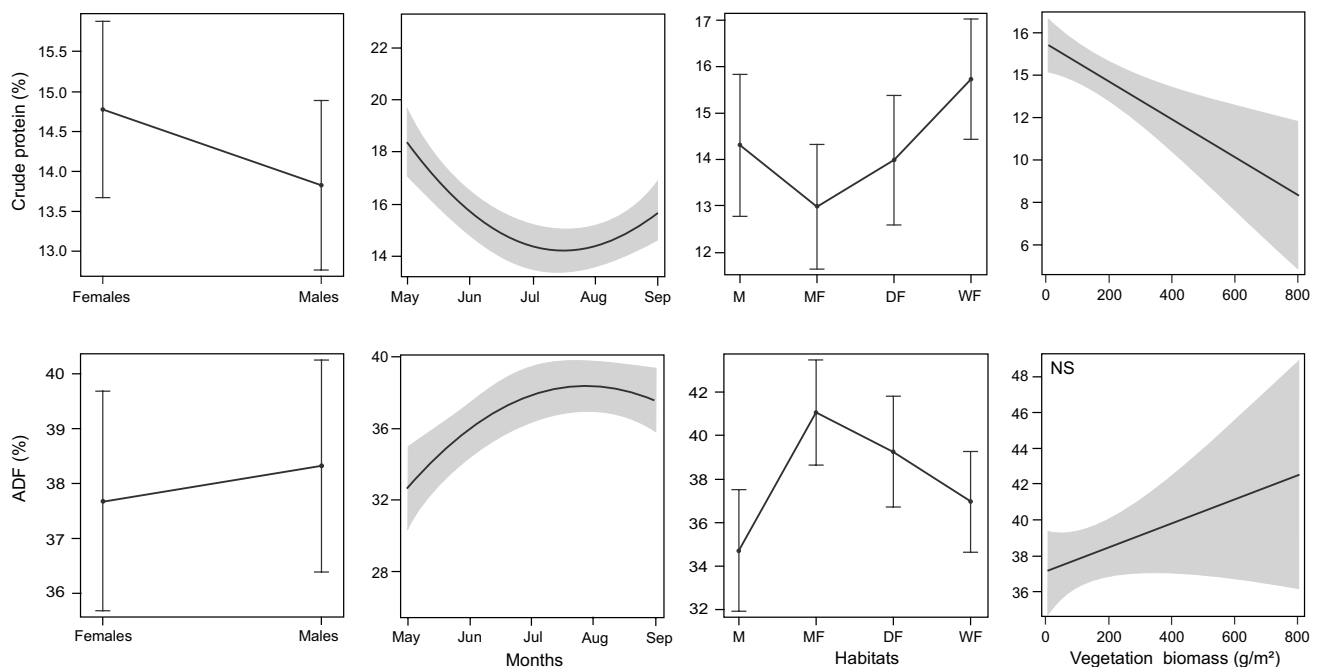
Results

We found no significant differences between males and females in the CP and ADF content of plant biomass collected within their food patches (Fig. 1). The quality of

Table 1 Parameter estimates for the generalized linear model with a Gaussian error structure (link "identity") testing the association between crude protein (CP) content and sex, habitat, month and biomass (GLM1)

Variable	Estimate ± SE	t	P
Sex			
Male (female)	− 0.95 ± 0.61	− 1.55	0.12
Month	− 0.72 ± 0.31	− 2.33	0.02
Month^2	1.26 ± 0.35	3.57	< 0.001
Habitat			
DF (MF)	1.02 ± 0.86	1.18	0.24
M (MF)	1.36 ± 0.89	1.52	0.13
WF (MF)	2.78 ± 0.81	3.42	0.001
M (DF)	0.33 ± 0.95	0.35	0.72
WF (DF)	1.75 ± 0.83	2.10	0.04
WF (M)	1.42 ± 0.87	1.63	0.11
Biomass	− 0.001 ± 0.003	− 3.31	0.001

Reference values for the factors analysed are given in brackets. Habitats: *MF* mixed forests, *DF* deciduous forests, *WF* wet forests, *M* meadows. ^ Exponentiation

Fig. 1 Predicted crude protein (CP) and fibre (ADF) content of plant biomass on European bison foraging patches in the Białowieża Primeval Forest. Based on results of GLM 1 and GLM 2. Whiskers and shaded areas denote 95% confidence intervals. Habitats: *M* meadows, *MF* mixed forests, *DF* deciduous forests, *WF* wet forests. *NS* not significant

the foraging patches varied significantly between months (Tables 1, 2). CP content was the highest in May, decreased until July–August, and increased slightly in September (Fig. 1), while the opposite temporal trend was observed for ADF. The highest quality patches were found in WF (CP = 15.7%), as the CP content was significantly higher than in MF (13.0%) and DF (14.0%) (Tables 1, 2, Fig. 1). The ADF content was significantly higher in MF (41.0%) than in M (35.9%) and WF (36.7%). We found significant negative association between CP content and biomass (Table 1, Fig. 1), while ADF content was not significantly related to biomass (Table 2, Fig. 1).

Mean vegetation biomass on European bison foraging patches (131.5 ± 12.3 g/m^2) was significantly lower than on random plots (210.5 ± 5.7 g/m^2) (Table 3). The difference was significant for all months. Vegetation biomass on bison foraging patches and random points increased from May to July, and decreased until September (Fig. 2).

We found significantly higher biomass selected by females than males (157.9 ± 155.1 and 102.6 ± 81.5 g/m^2, respectively) (Student's t-test: $t = 2.36$, $P = 0.02$).

Discussion

Our analyses showed that the quality of the foraging patches used by European bison showed no significant sex differences, and both sexes selected patches with significantly lower vegetation biomass than random.

Despite large sexual dimorphism in body size, we found no support for the Jarmann–Bell principle in European

Table 2 Parameter estimates for the generalized linear model with a Gaussian error structure (link "identity") testing the association between fiber (ADF) content and sex, habitat, month and biomass (GLM2)

Variable	Estimate ± SE	t	P
Sex			
Male (female)	0.64 ± 1.11	0.57	0.57
Month	1.46 ± 0.56	2.62	0.01
Month^2	− 1.30 ± 0.64	− 2.04	0.04
Habitat			
DF (MF)	− 1.79 ± 1.57	− 1.14	0.25
M (MF)	− 6.33 ± 1.62	− 3.91	< 0.001
WF (MF)	− 4.10 ± 1.47	− 2.78	0.01
M (DF)	− 4.54 ± 1.71	− 2.65	0.01
WF (DF)	− 2.30 ± 1.51	− 1.52	0.13
WF (M)	2.24 ± 1.58	1.42	0.16
Biomass	0.01 ± 0.005	1.38	0.17

Reference values for the factors analyzed are given in brackets. Habitats: *MF* mixed forests, *DF* deciduous forests, *WF* wet forests, *M* meadows. ^ Exponentiation

Table 3 Parameter estimates for the generalized linear model with a gamma error structure (link "log") testing for differences in biomass between plots visited by European bison and random sites in different months (May–September) (GLM 3)

Variable	Estimate ± SE	Test statistics	P
Month	0.06 ± 0.08	0.76	0.45
Month^2	− 0.30 ± 0.09	− 3.37	0.001
Plot type			
Random (utilized by bison)	0.43 ± 0.12	3.47	0.001
Month * plot type	0.04 ± 0.09	0.45	0.65
Month^2 * plot type	0.06 ± 0.09	0.61	0.54

^ Exponentiation; * Interaction

bison. This finding is consistent with our previous DNA-based analysis of the diet of European bison, which did not confirm substantial differences in the composition of plant species consumed by females and males (Kowalczyk et al. 2019).

As diet quality approaches a threshold beyond which animals with a certain metabolic rate/gut capacity ratio cannot extract enough energy from the diet to survive, animals begin to become more selective and seek out the high-quality food patches (Pérez-Barbería et al. 2008). Thus, intraspecific dietary segregation should occur when one of the sexes is limited in its ability to digest the same food due to sex-specific metabolic rate/gut capacity ratios. In habitats where the food quantity and quality do not limit the metabolic rate/gut capacity ratio of both sexes, limited or no
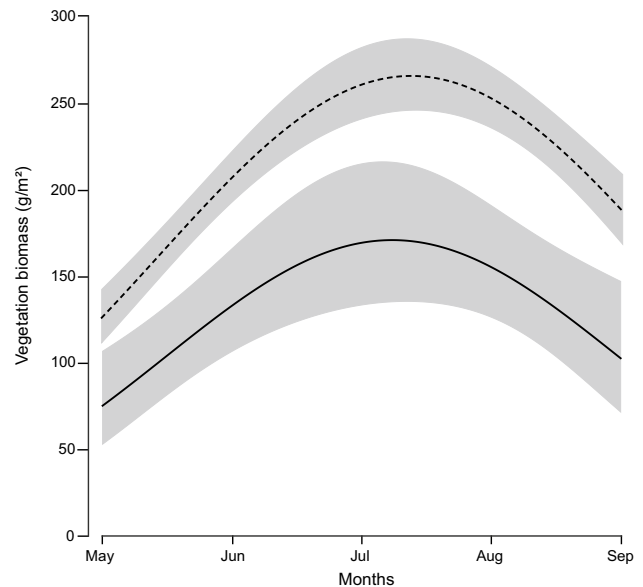
Fig. 2 Predicted biomass of vegetation on European bison foraging patches (solid line) and random plots (dashed line) in different months in the Białowieża Primeval Forest. Based on results of GLM 3. Shaded areas denote 95% confidence intervals

dietary segregation is expected (Pérez-Barbería et al. 2008). This explanation may also apply to European bison using the rich habitats of the BPF.

Forest habitats have been recognised as suboptimal for European bison, which are better adapted to more open habitats (Mendoza and Palmqvist 2008; Kerley et al. 2012). This is mainly due to the limited availability of forage in forest habitats from autumn to early spring, when there is little herbaceous vegetation on the forest floor. However, during the growing season, rich deciduous and wet forests provide large amounts of highly digestible forage such as herbs, ferns and leaves of woody vegetation (Kowalczyk et al. 2019). Our study showed that foraging patches in wet and deciduous forests were of higher quality than those on meadows. In the forest habitats, European bison are opportunistic generalists that continuously adapt their diet to seasonal changes in the availability of easily digestible non-grass vegetation (Kowalczyk et al. 2019). It appears that the high patch quality and diet plasticity of European bison limits sex segregation in the rich habitats of the BPF.

Interestingly, diet segregation was found in closely related American bison—faecal analysis revealed higher diet quality in American bison females, while males had greater diet breadth (Berini and Badgley 2017). However, unlike European bison, American bison inhabit more open habitats dominated by less digestible graminoid vegetation (Knapp et al. 1999; Jorns et al. 2020), which is likely to result in greater forage selectivity.

We found significantly higher biomass selected by females, although there were no differences in the quality of food patches selected by the two sexes. This may be related to grouping behaviour and predation risk. Females, unlike males, usually feed in herds and may require higher biomass of vegetation, but still of higher quality and well below randomly available biomass, to satisfy all herd members. Although predation accounts for only a small proportion of bison mortality (Jędrzejewski et al. 2000), the risk is particularly high for female groups, as predation mainly affects younger bison (Kowalczyk R, unpublished). When foraging in patches of higher biomass, vigilance may be exercised in the time used to chew bites that have already been cropped (Illius and Fitzgibbon 1994). On low biomass patches cropping and chewing may occur simultaneously, slowing or stopping foraging when the head is raised for vigilance (Laca et al. 1994). Stronger selection for meadows with higher vegetation biomass by larger groups was found in American bison, indicating a trade-off between food availability and predation risk (Fortin et al. 2009).

As plant biomass matures and the composition and structure of cell walls change, the forage digestibility and passage rates decrease (Spalinger and Hobbs 1992; Gross et al. 1996). Thus, ungulates are forced to select forage of intermediate biomass and digestibility to maximise energy intake, as suggested by the FMH. In our study, forage acquisition by European bison followed this pattern. Bison selected for patches of significantly lower biomass than randomly available and CP content significantly decreased with increasing vegetation biomass. Selection for a low or intermediate levels of vegetation biomass has also been reported in closely related American bison (Raynor et al. 2016). Interestingly, the FMH, originally developed to explain forage resource selection in tropical bulk-grazing ruminants, has also found support in temperate herbivores occupying both open (Mueller et al. 2008; Raynor et al. 2016) and forested habitats (this paper).

In contrast to open habitats, where vegetation structure, phenology and maturation are less variable in time (Bruinenberg et al. 2002; Horbach et al. 2023), in forest habitats, patch selection by European bison is driven by the higher variability in the plant community among habitat patches and phenology of different plant species that develop and flower at different times during the growing season (Jaroszewicz et al 2009; Sparks et al. 2009; Kowalczyk et al. 2019). Thus, the mosaic structure and great diversity of plant species in the BPF, where deciduous and wet forests with rich undergrowth and river valley support hundreds of vascular plant species, allows these large herbivores to optimize their selection.

European bison have been recognized as a refugee species in non-optimal forest habitats. However, forest habitats of the BPF during the growing season provide European bison with sufficient biomass of high quality forage (Kowalczyk et al. 2019). The foraging plasticity of European bison, allows this grazing-adapted herbivore to continuously adapt its diet to non-grass forage throughout the year (Kowalczyk et al. 2011, 2019). However, this may vary across the range of European bison, as most populations inhabit poor coniferous forests (Kerley et al. 2012). In these areas, European bison are often supplemented in winter, which is costly and has negative effects on animal behaviour and health, increasing habituation and parasite infestation (Radwan et al. 2010; Kerley et al. 2012; Haidt et al. 2018; Kołodziej-Sobocińska et al. 2016). Therefore, the evaluation of suitable areas for bison reintroduction should include an assessment of both vegetation availability and quality. Understanding the relationship between forage selection by European bison and forage nutritional constraints in forest habitats may be crucial for conservation programmes for this species.

Author contributions All authors contributed to the study conception and design. Data collections were performed by RK and TK. Analysis

was performed by TB and RK. The manuscript was written by RK and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability The authors confirm that the data presented and analysed in this article have been deposited in an open repository Open Forest Data and can be accessed at: https://doi.org/10.48370/OFD/XY6WHQ.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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