Latitudinal and seasonal plasticity in American bison *Bison bison* diets

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ABSTRACT

1. In ecological niche theory, diet is a trait frequently used to place species along a continuum from specialists to generalists. A multidimensional approach to investigating species' niches has been developed to incorporate nutrition. We apply the concepts of multidimensional nutritional niche theory to the dietary patterns of a widespread, large herbivore, the American bison *Bison bison*, at various levels of its nutritional niche.
2. Specifically, we sought to estimate dietary niches for female bison at the levels of the forage items they consume and the macronutrients they acquire from those forage items. We assessed how these dietary niches changed seasonally and explored physical and climatic mechanisms that contribute to observed differences in the dietary niches. We also examined dietary differences between the two bison subspecies: wood bison *Bison bison athabascae* and plains bison *Bison bison bison*.
3. We compiled data for 16 bison subpopulations using 26 peer-reviewed publications, government reports, conference proceedings, and graduate theses that described the dietary composition of female bison for analysis of dietary niches.
4. We found that the diets of female bison were, as expected, dominated by graminoids throughout the year, but during the growing season (spring and summer), dietary niches had greater breadth. Their diets were relatively high in carbohydrates, but percentages of dietary lipid and protein increased during the growing season. Further, we found significant increases in consumption of browse items, lipids, and proteins with increasing latitude (°N), and differences between American bison subspecies.
5. Our study provides insight into the fundamental macronutrient niche of the American bison and also provides a framework for the nutritional targets of bison. We show that bison are able to adapt to availability of local forage and that they may consume different items in different proportions in order to regulate nutritional composition of their diet.

INTRODUCTION

The ecological niche is a foundational concept in ecological and evolutionary theory. In the context of niche theory, diet is a trait consistently used to place species along a scale of niche breadth from specialists to generalists (Terraube et al. 2014). A multidimensional approach known as nutritional geometry has been advanced to incorporate dietary nutrition in ecological niche theory (Machovksi-Capuska et al. 2016). This approach allows for the characterisation of a species' dietary niche within different functional (i.e. adaptive; Bateson & Laland 2013) levels, which are known as: the food exploitation niche, food composition niche, realised macronutrient niche, and fundamental macronutrient niche.

The food exploitation niche explores the physical and ecological traits of food items (e.g. food type, part of food item eaten, or seasonal availability). For example, foods with hard exteriors (e.g. nuts) may not be available for consumption by some species due to their physical characteristics, and foods that occur below ground (e.g. roots) may not be ecologically available to non-digging species. The food composition niche characterises the macronutrient (e.g. protein, lipid, and carbohydrate) compositions found within the food items an animal consumes. The realised macronutrient niche characterises the macronutrient compositions of foods actually consumed at a given place and time, integrating biological limitations on food availability, such as competition and seasonal fluctuations in the quantity and quality of foods. The fundamental macronutrient niche estimates the range of macronutrient compositions in a species' diet that allows for population persistence (Coogan et al. 2018a). Understanding nutritional niche at these different levels is important for understanding ecological relationships between diet and nutrition, with practical implications for species conservation and management (Coogan et al. 2018b, Panthi et al. 2019).

Species that are dispersed across geographically wide and ecologically diverse ranges may have diverse diets, especially in terms of the food items consumed by geographically distinct populations (Senior et al. 2016). However, geographically driven diversity in food items consumed between populations does not necessarily correspond to dietary differences in macronutrient composition (i.e. realised macronutrient niches). For example, in herbivorous mountain gorillas *Gorilla beringei,* two geographically disjunct populations forage on different plant species, but acquire a consistent composition of macronutrients (Rothman et al. 2011). These results suggest a degree of generalisation in types of foods consumed, yet specialisation in the preferred proportion of dietary macronutrients consumed. The opposite pattern was observed in invasive, omnivorous wild boars *Sus scrofa*, which showed high plasticity in the macronutrient composition of the types of foods consumed, the macronutrient composition of those foods, and the macronutrient balance of their diets, both geographically and seasonally (Senior et al. 2016). Thus, wild boars were considered to have relatively wide food exploitation, food composition, and fundamental macronutrient niches. Therefore, understanding an animal's feeding strategies requires knowledge of the breadth of foods available and exploited, and the macronutrients acquired through those foods.

American bison *Bison bison* were once nearly ubiquitous throughout North America, with a geographic range spanning roughly from the Rocky Mountains east to the Appalachians, and from northern Mexico north into the boreal forests of Alaska and the Yukon (Cunfer & Waiser 2016). While their distribution has become more fragmented after near extirpation in the 19th Century, bison still occupy a diversity of habitats in North America. Throughout their range, bison have been thought of as obligate grazers (Strong & Gates 2009). However, there is a growing body of evidence that suggests bison diets include substantial quantities of forbs and shrubs (Bergmann et al. 2015, Craine et al. 2015, Leonard et al. 2017, Jorns et al. 2019). The variation in bison diets is poorly understood. By investigating the nutritional niche of bison at multiple levels, we will assess how changes in the food items bison consume relate to the macronutrients that they acquire. By applying this approach, we go beyond the traditional crude protein and digestibility measure of nutritional quality, to shed light on potential macronutrient ratio targets that characterise bison diets. We therefore investigate the bison's diet through the lens of multidimensional nutritional niche theory to improve our understanding of bison nutritional ecology.

We review the frequency of different functional forage groups (i.e. graminoid, forb, and browse items) in the diets of female bison throughout North America, and record whether or not differences in foods consumed resulted in differences in macronutrient composition. Our objectives are to: 1) examine the food exploitation (differences in consumption of graminoids, forbs, and browse), food composition (estimated macronutrient contents), and realised macronutrient niches (macronutrient composition of subpopulation diets) for bison, thereby providing insight into their fundamental macronutrient niche; 2) assess how these niches change seasonally; 3) investigate how environmental variation in habitat may relate to changes in food or macronutrient consumption; and 4) test for differences between the diets of the two subspecies of American bison: plains bison *Bison bison bison* and wood bison *Bison bison athabascae*. We will meet these objectives through a review of studies that quantify the proportions of forage

items in bison diets based on faecal analyses and direct observations, and by using literature estimates of the macronutrient compositions of foods consumed. Regarding the food exploitation niche, we predict that female bison diets will be higher in graminoids than forbs or browse. However, the degree of variation in the percentages of functional forage groups should differ between subpopulations. As bison are ruminant herbivores, their digestive systems are adapted to acquire energy from low-quality food items; therefore, we anticipate that bison will have relatively narrow macronutrient niche breadths. However, the variety of macronutrients available in foods consumed by female bison should expand, as a wider variety of forage items becomes available during the growing season (i.e. spring and summer). We predict that there will be differences among the macronutrient percentages of subpopulation diets, due in part to differences in the types and amounts of foods available. The range of realised niches created from each subpopulation will provide an estimate of the fundamental macronutrient niche for American bison. Furthermore, we will investigate how the physical and climatic conditions of each subpopulation's location influence the items foraged by the bison and macronutrients acquired, while controlling for differences in method of diet analysis.

METHODS

Literature review and macronutrient estimates

We conducted a review of available literature using the search engines Google Scholar and Web of Science. We used the keyword 'bison' with 'diet', 'diet composition', 'microhistology', 'faecal analysis', or 'faecal composition' to locate peer-reviewed articles that reported results of bison diet composition analyses in terms of relative bulk of forage items in bison diets. When an article was located, we scoured the literature cited within it for additional peer-reviewed articles. We found 26 articles, including published peer-reviewed articles and book chapters ($n = 21$), graduate theses ($n = 3$), government reports ($n = 1$), and conference proceedings ($n = 1$) that represented 16 bison subpopulations throughout North America (Fig. 1). When studies differentiated male and female diets, we only used the female diet, and we consider our results to be estimates of female dietary niches. Given that we investigated differences in bison diets based on their geographic location, we avoided pseudo-replication by pooling all studies conducted on the same herd (Remonti et al. 2015; Table 1).
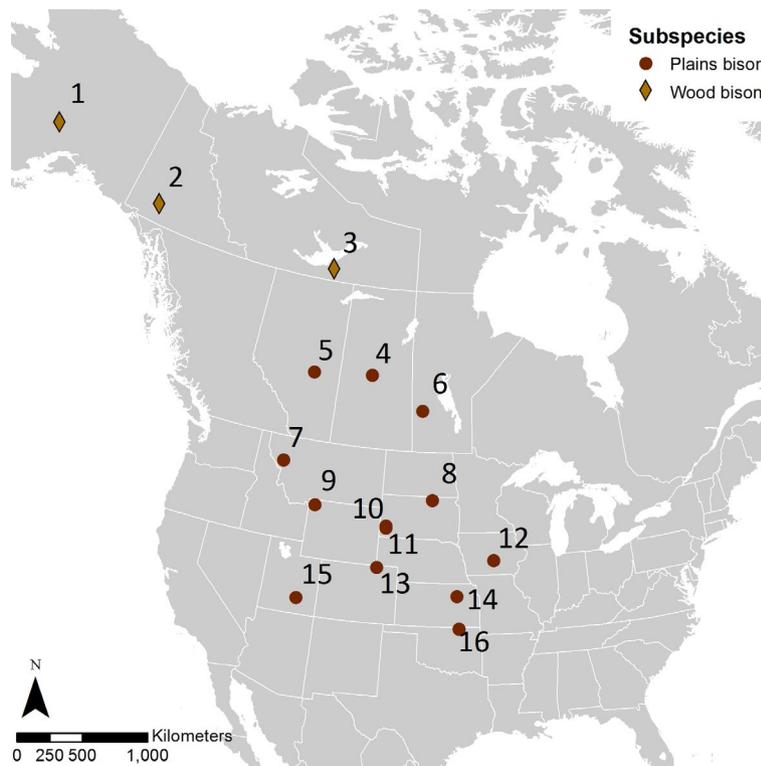

Fig. 1. Distribution of the 16 American bison *Bison bison* herds used in this review of bison diets. Point symbols indicate herds located in the historic geographic range of plains bison *Bison bison bison*, while diamond symbols represent herds in the historic geographic range of wood bison *Bison bison athabascae*. Numbers refer to each unique bison herd (Table 1).

Table 1. A summary of the female bison subpopulations used for dietary niche analyses including the location of the subpopulation, citations for the studies of where diet information was acquired, and the seasons covered in those studies. Studies that reported growing and non-growing season dietary compositions were used in analysis of annual diets. Subpopulations are listed in order of their latitudinal location (most northern to most southern), and the codes listed in the leftmost column are used to identify each herd in all figures.

Code	Location	Seasons	Subspecies	Literature
1	Farewell Lake, Alaska, USA	Growing Non-growing	*B. b. athabascae*	Campbell and Hinkes (1983) and Waggoner and Hinkes (1986)
2	Aishihik Lake, Yukon, Canada	Growing Non-growing	*B. b. athabascae*	Fischer and Gates (2005), Jung (2015) and Jung et al. (2015)
3	Slave River Lowlands, Northwest Territories, Canada	Growing Non-growing	*B. b. athabascae*	Reynolds et al. (1978)
4	Prince Albert National Park, Saskatchewan, Canada	Growing Non-growing	*B. b. bison*	Fortin et al. (2002)
5	Elk Island National Park, Alberta, Canada	Growing Non-growing	*B. b. bison*	Holsworth (1960), Telfer and Cairns (1979)
6	Pine River Ranch, Manitoba, Canada	Growing	*B. b. bison*	Leonard et al. (2017)
7	National Bison Range, Montana, USA	Growing	*B. b. bison*	Mooring et al. (2005)
8	Samuel H. Ordway Jr. Memorial Prairie, South Dakota, USA	Growing	*B. b. bison*	Plumb and Dodd (1993)
9	Yellowstone National Park, Wyoming, USA	Growing Non-growing	*B. b. bison*	Meagher (1973) and Delguidice et al. (2001)
10	Wind Cave National Monument, South Dakota, USA	Growing Non-growing	*B. b. bison*	Popp (1981) and Krueger (1986)
11	Custer State Park, South Dakota, USA	Growing	*B. b. bison*	Keller (2011)
12	Neal Smith National Wildlife Refuge, Iowa, USA	Growing	*B. b. bison*	Kagima and Fairbanks (2013)
13	Pawnee National Grassland, Colorado, USA	Growing Non-growing	*B. b. bison*	Peden et al. (1974), Peden (1976), Kautz and van Dyne (1978) and Schwartz and Ellis (1981)
14	Konza Prairie Preserve, Kansas, USA	Growing	*B. b. bison*	Bergmann et al. (2015)
15	Henry Mountains, Utah, USA	Growing	*B. b. bison*	van Vuren and Bray (1983) and van Vuren (1984)
16	Tallgrass Prairie Preserve, Oklahoma, USA	Growing Non-growing	*B. b. bison*	Coppedge et al. (1998)

Next, we collected data on the macronutrient content of foods consumed by bison, measured in percent composition of lipids, proteins, and carbohydrates, for each species reported in the female bison's diet, primarily using Duke and Atchley (1986) and Feedipedia (https://www.feedipedia.org/). For studies that reported percent composition of bison diets in terms of functional forage groups (i.e. graminoids, forbs, and browse), we used mean macronutrient content of dominant species within the study area for each functional forage group. While using macronutrient estimates from the literature may be a crude approach to estimating macronutrient content of food items, such an approach is useful when making dietary comparisons between groups of animals and is an informative method for studying comparative nutritional ecology (Remonti et al. 2016, Senior et al. 2016, Coogan et al. 2017). We then converted macronutrient content of individual foods to metabolisable energy values using appropriate conversion factors: 9 kcal g^{-1} for lipids; 4 kcal g^{-1} for proteins; and 4 kcal g^{-1} for carbohydrates (Merrill & Watt 1973). Metabolisable energy values for each macronutrient were expressed as the percentage of total metabolisable energy that was derived from that macronutrient. We

estimated dietary macronutrient percentages by weighting percent metabolisable energy estimates for food items by their frequency of occurrence in the bison's diet (Coogan et al. 2018a). We also examined metabolisable energy values for three functional forage groups for bison: graminoids (loosely defined as all sedges and grasses with C3 and C4 photosynthetic pathways), forbs, and browse items.

Multidimensional nutritional niche

We used right-angled mixture triangles (RMTs) to visualise patterns in the percentages of macronutrients in foods and diets of bison (Raubenheimer 2011). The RMT is a multivariate graphical approach, with an accompanying theoretical framework, that has been implemented to examine nutritional ecology in both natural and experimental settings (Raubenheimer et al. 2015a, b). In particular, RMTs are useful for visualising and modelling macronutrients in a three-dimensional simplex. To investigate food composition and realised macronutrient niches, we constructed RMTs with protein composition on the *x*-axis, lipid composition on the *y*-axis, and carbohydrate composition on the implicit

(*z*-axis) access. We generated RMTs to evaluate the macronutrient percentages in the diets of subpopulations of bison (realised macronutrient niches) during the growing season (April–September), non-growing season (January–March), and the whole year (annual diets). We only found two studies (Larter & Gates 1991, Larter & Allaire 2007) that described bison diets in the autumn and early winter, so, for consistency, we defined our non-growing season as occurring from January to March. For RMTs describing realised macronutrient niches, we generated convex hull polygons around points representing each herd's realised macronutrient niche, to provide insight into the bison's fundamental macronutrient niche.

We analysed the percentages of macronutrients that account for the greatest variance in bison diets using a principal component analysis for compositional data (Filzmoser et al. 2009), implemented in the package 'compositions' (van den Boogaart et al. 2018) in R version 3.6.1 (R Core Team 2019). Using biplots, we graphically examined the variance between components by looking at the length of each link (i.e. the difference between the ends of each line), which represents the standard deviation of the log ratio of two components; longer links indicate greater variance accounted for by the ratio of those two components.

Environmental factors affecting realised macronutrient niches

To investigate how the physical and climatic conditions of subpopulation location influence the food exploitation and realised macronutrient niches of bison, we created a series of linear models for annual, growing season, and non-growing season diets. Because we used compositional data, we used isometric log ratios of forage groups and macronutrient compositions as response variables (Aitchison 1982, Coogan et al. 2018b) in the R package 'compositions' (van den Boogaart et al. 2018). For the food exploitation niche, graminoids were used as the denominator in log ratios, and for the realised macronutrient niche, we selected carbohydrates as the denominator in log ratios. We selected three uncorrelated covariates as the predictors for our models: latitude, elevation, and precipitation (seasonality of precipitation for annual diets and the mean value of monthly precipitation during growing and non-growing seasons). Precipitation data were acquired from the WorldClim database (Hijmans et al. 2005). Temperature variables such as mean annual temperature were correlated with latitude and performed worse in exploratory models. We therefore excluded temperature variables. Latitude, elevation, and method of diet analysis were acquired from each study. Four models for each season were generated with forbs and browse used as the

numerators in the food exploitation niche analyses, and lipids and proteins in the realised macronutrient niche analyses. Method of diet analysis was used as a random effect to control for differences in reported diet composition due to dietary analysis methods. After models were generated, we back-transformed the coefficients for each predictor so that the results can be interpreted as the amount of change in the ratio of forage groups or macronutrient per one unit change in the predictor (Tolosana-Delgado & van den Boogaart 2011).

Lastly, we used simple significance tests (one-way Student's *t*-tests; Ramsey & Schafer 2002) to assess differences in dietary composition between plains bison and wood bison. Genetic studies have shown that it is unlikely that 'pure' wood bison still exist in the wild, as reintroductions of plains bison into what was wood bison range have led to genetic introgression (Ball et al. 2016). Therefore, we consider wood bison herds to be those that fall within the historic geographic range of the wood bison, and plains bison to be herds that are located within the historic geographic range of the plains bison (Cunfer & Waiser 2016).

RESULTS

Food exploitation niche

Graminoids were the dominant forage item [mean = 85%, standard deviation (SD) = 25] found in annual female bison diets, with forbs contributing slightly more (8.5%, SD = 15) than browse (6.7%, SD = 12). During the growing season, graminoids were still the dominant forage item (mean = 83%, SD = 27); forbs (mean = 8.7%, SD = 18) and browse (mean = 8.6%, SD = 15) made up similar percentages. In the non-growing season, graminoids were again the dominant forage item (mean = 88%, SD = 23), followed by forbs (6.3%, SD = 12) and then browse (mean = 5.9%, SD = 14).

Food composition and realised macronutrient niches

Overall, bison had a relatively narrow food composition niche with most of the metabolisable energy in their foods coming from carbohydrates (Fig. 2a). However, several foods were relatively high in lipids (providing approximately 25–35% of the metabolisable energy), while no food items exceeded 30% metabolisable energy from proteins. Annually, browse items contributed to the largest percentage of lipids to bison diets, and forbs contributed the largest percentage of protein (Fig. 3). Overall, the mean percentages of metabolisable energy from macronutrients in annual bison diets were as follows: 82% (SD = 2.8) carbohydrates, 7.2%
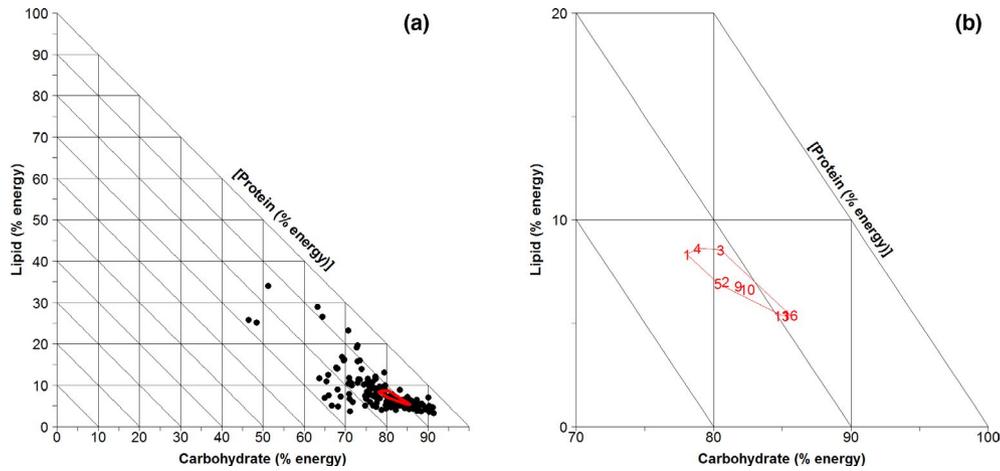
Fig. 2. (a) Right-angled mixture triangle (RMT) depicting the macronutrient compositions of forage items (food composition niche or macronutrient niche breadth) identified in female bison diets in North America (*n* = 192 unique species foraged; circles on plot) expressed as a percentage of metabolisable energy. The convex polygon shows the region of the simplex outlining each herd's realised macronutrient niches, thereby providing insight into the breadth of bison's fundamental macronutrient niche relative to the range of macronutrient compositions in foods consumed. (b) A close-up of the realised macronutrient niches of each bison herd in North America based on annual diets. Each number represents a single herd's realised macronutrient niche, and the convex polygon provides an estimate of American bison's *Bison bison* fundamental macronutrient niche. Numbers refer to each unique bison herd (Table 1).
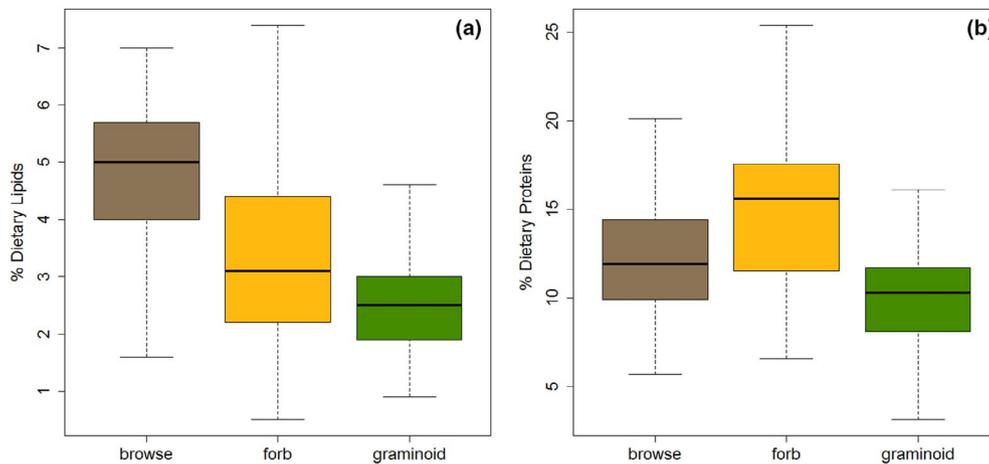

Fig. 3. Box plots of the functional forage groups and their relative annual contribution towards (a) percent lipids and (b) percent proteins, in female bison diets. The bold line inside each box represents the median percentage of the macronutrient from each forage group, while the box itself represents the interquartile range. The whiskers extending from each box show the range of percentages for each macronutrient in each forage group.

(SD = 1.2) lipids, and 11% (SD = 1.9) proteins (Fig. 2b). The coefficient of variation for each macronutrient was 3.4% for carbohydrates and 17% for both lipids and proteins, demonstrating that carbohydrates varied the least relative to their mean percentages. The realised dietary niches of subpopulations were clustered in the RMT simplex, despite variation in the composition of food items, suggesting a relatively narrow fundamental macronutrient niche. The principal component analysis demonstrated that the lowest variation between macronutrient ratios occurred for the proteins:lipids ratio (Fig. 4), while the highest variation in macronutrient ratios was observed between both the carbohydrates:lipids and the carbohydrates:proteins ratios.

Differences between annual diet and growing season diet composition were nominal: bison diets were composed of 81% carbohydrates (SD = 2.8), 7.3% lipids (SD = 1.3), and 11% proteins (SD = 1.8) in the growing season. Between the non-growing season and annual diets, differences in macronutrient composition were also nominal: 82% of the metabolisable energy came from carbohydrates
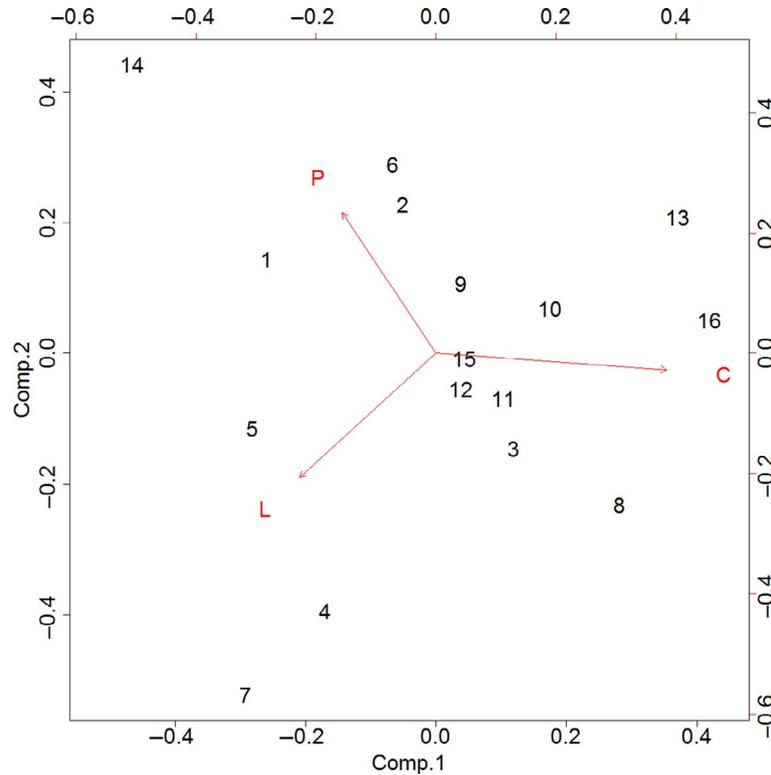
Fig. 4. Biplot visualising a compositional principal component analysis of the percentage of metabolisable energy from macronutrients in American bison *Bison bison* diets. The length of each link (i.e. the difference between the ends of each line) signifies the standard deviation of the log ratios between two components. Therefore, the length of each link represents the variation between two components. Numbers refer to each unique bison herd (Table 1). P = protein; L = lipid; C = carbohydrate.

(SD = 2.5%), 6.9% from lipids (SD = 1.1%), and 12% from proteins (SD = 1.6) in the non-growing season. Macronutrient niche breadth of bison diets during the growing season was 2.8 times greater than that during the non-growing season, based on differences in the volume of convex hull polygons surrounding diet estimates (Fig. 5).

Environmental factors affecting niches

Visual examination of the effect of method of diet analysis on the composition of forage groups in bison diets showed differences in forage groups identified among methods. However, the estimated macronutrient percentages of bison diets remained relatively constant despite different methods of diet analysis (Fig. 6). Including the method of diet analysis as a random effect did not improve the fit of linear regression models, except for models of forage group ratios during the growing season. Therefore, we used linear regressions for all other models. The annual models revealed a significant positive relationship between percent browse:graminoids ratio and latitude (°N), with a 1.23% increase per 1° increase in latitude, and a significant increase of 1.02% lipids:carbohydrates ratio per 1° of latitude (Table 2; Fig. 7). Similarly, there was

a significant increase of 1.02% per 1° of latitude for lipids:carbohydrates ratio in growing season diets. Non-growing season diets had a marginally significant increase of 1.17% in the browse:graminoids ratio, with a 1° increase in latitude, and a marginally significant increase of 1.02% in lipids:carbohydrates ratio per 1° increase in latitude.

Wood bison vs. plains bison

We found significant differences in diet between plains and wood bison subspecies. Plains bison consumed significantly less browse ($t = -3.070$, $P = 0.003$), lipids ($t = -2.748$, $P = 0.007$), and proteins ($t = -1.831$, $P = 0.041$) than wood bison. We found no significant difference in the consumption of graminoids, forbs, or carbohydrates between the two subspecies.

DISCUSSION

We used a multidimensional nutritional niche framework to examine the nutritional ecology of female American bison. Regarding the food exploitation niche, large herbivorous bison are limited in the varieties and types of foods consumed in comparison with, for example,
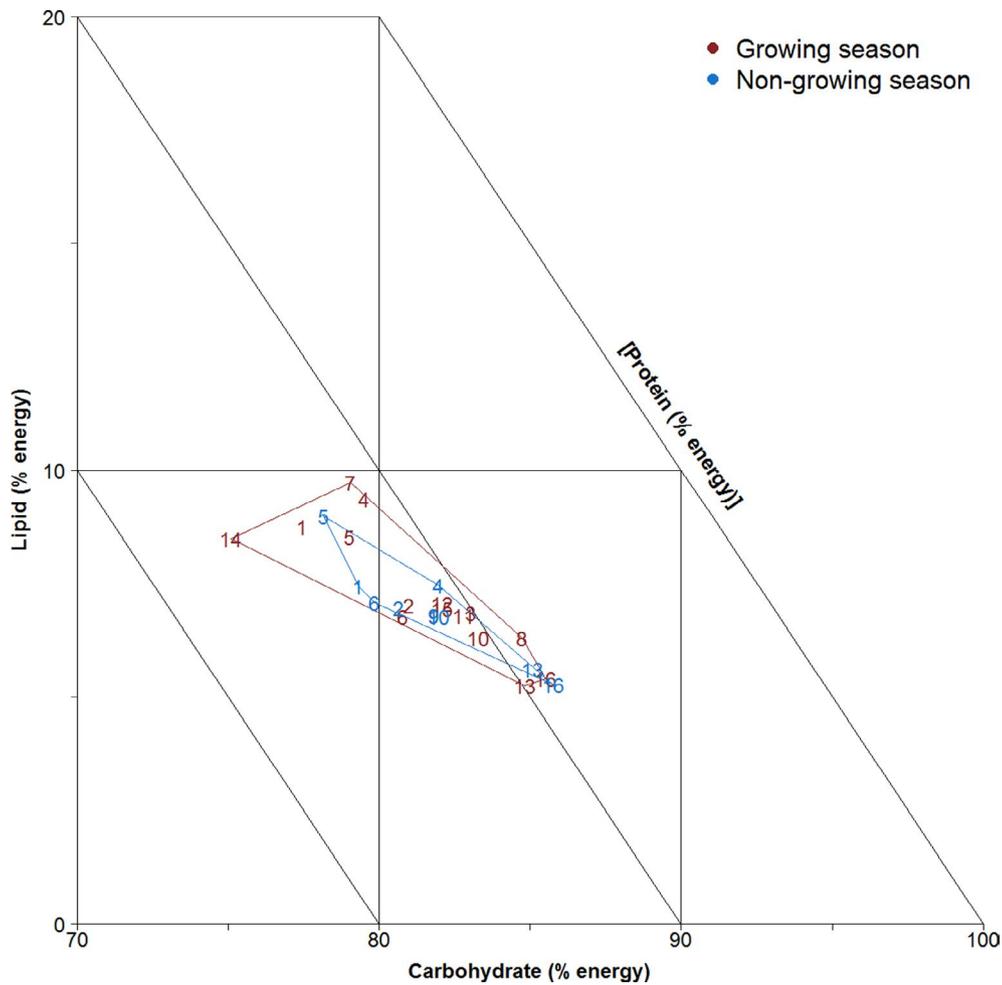
Fig. 5. Right-angled mixture triangle showing a close-up of the seasonal percentages of dietary macronutrients (realised macronutrient niches) for female American bison *Bison bison* herds in the growing and non-growing seasons. Numbers refer to each unique bison herd (Table 1).

omnivorous mammals that consume a variety of animal prey items and vegetative foods. Greater dietary variety also results in omnivores having wider food composition niches. For example, brown bears *Ursus arctos* can consume a variety of high-protein and high-lipid animal-based foods, in combination with high-carbohydrate foods, resulting in wide food composition niches, and can also tolerate a relatively wide range of realised diet niches (Coogan et al. 2017). Obligate carnivores, such as feral cats *Felis silvestris*, consume primarily animal prey and have been shown to self-select diets that are primarily composed of proteins (52% of daily energy intake) and lipids (46%), with only minimal amounts of carbohydrate (2%; Plantinga et al. 2011). In contrast, bison and other ungulates are generally restricted to browse, forb, and graminoid-based diets. However, bison show flexibility in the proportions of each type of functional forage group they consume, depending on the ecosystem they are in. Furthermore,

diets of bison were relatively high in the percentage of available carbohydrate consumed, which reflects the range of dietary food items they have evolved to forage on.

Bison's realised diet niches occupied a restricted space of the RMT simplex relative to the macronutrient breadth of food items, suggesting that, like many other animals, bison regulate their intake of food items homeostatically, in order to consume a preferred proportion of dietary macronutrients (Simpson et al. 2004). We did not examine the availability of food items to establish whether bison were selecting food items disproportionately to their availability. However, given that macronutrient balancing through differential consumption of food items is a well-established biological phenomenon, our suggestion is not unfounded (Simpson & Raubenheimer 2012). Furthermore, a diet that contains macronutrients in proportion to the available food items does not necessarily mean that an animal forages unselectively. Animals may follow rules of
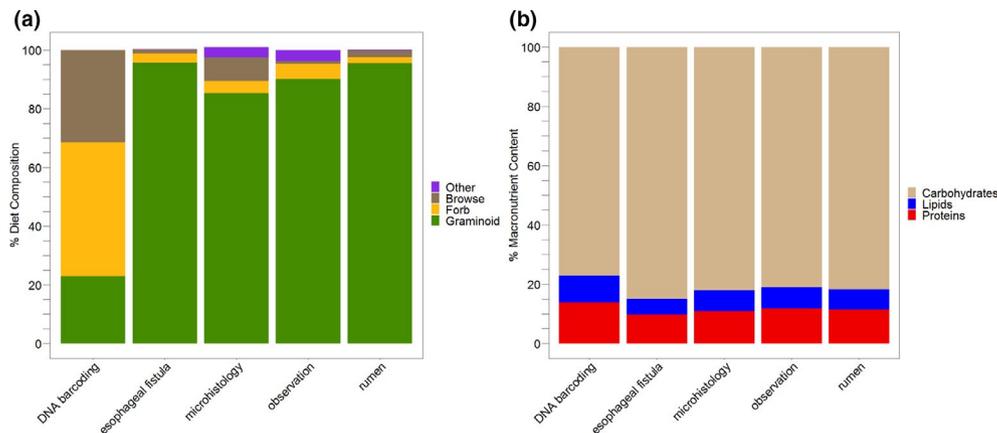
Fig. 6. Bar charts showing differences in (a) the functional forage group (% diet composition) and (b) the percentage of metabolisable energy derived from each macronutrient (% macronutrient content) in American bison *Bison bison* diets, depending on the method used to analyse the diet.

compromise, which guide their foraging decisions in the face of an unbalanced diet, or may have evolved macronutrient preferences based on the proportional availability of food items. The clustering of realised diet niches within the RMT simplex that we found for bison suggests a similarly small range of fundamental macronutrient niches that a bison population could persist on. Thus, while variation exists in the percentage of macronutrients in bison diets, we are unable to determine the source of that variation definitively. We also acknowledge that our study was focused on female bison, which generally have higher quality diets than males (as shown by analysis of stable nitrogen isotopes in faecal samples; Berini & Badgley 2017). Our macronutrient estimates would probably have included greater amounts of carbohydrates, resulting in a narrower dietary niche, if males had been included.

As the largest extant terrestrial herbivore in the Americas, bison are well adapted to have diets dominated by low-quality graminoids (Mooring et al. 2005). The extended rumination time of their large body allows bison to get the most out of these food items (Barboza & Bowyer 2000). The high-carbohydrate diet of bison is similar to that found for other large herbivores. For example, blue sheep *Psuedois nayaur* in Nepal also have a diet dominated by graminoids, with corresponding high levels of carbohydrates (Aryal et al. 2015). We found that the diets of American bison increased in lipids and proteins as the proportions of browse and forb items increased in the diet. In the river flood plains of Alaska, which are dominated by shrubs, particularly willows *Salix* spp., over 90% of the bison's diet is composed of browse items (Waggoner & Hinkes 1986). The European bison *Bison bonasus* (the closest living relative to American bison), considered to be a refugee species as its range is limited to protected forested areas, also has a growing season diet that is dominated by forbs and browse items (Kowalczyk et al. 2011). Having a greater amount of protein and moisture may make forbs and browse more readily digestible and palatable than graminoids for bison (Craine 2009). Aryal et al. (2015) examined the balance of fibre in the diets of blue sheep and found that the sheep tended to forage on plants higher in hemicellulose, which is likely to be relatively easily digestible. Therefore, examining the fibre-derived energy in bison diets may yield additional insight into their nutritional ecology. Other aspects of plant ecology, not considered here, may influence a herbivore's foraging, such as concentrations of secondary compounds, and grazing and fire regimes; these aspects require further consideration (Hudson & White 1985). However, macronutrients have been shown to drive the foraging behaviour of several species and are generally correlated with fibre content and other micronutrients (Simpson & Raubenheimer 2012).

The over twofold increase in macronutrient dietary breadth in growing season diets compared to non-growing season diets is consistent with the greater variety of foods available to bison during the growing season. Though not directly addressed in this study, evidence suggests that, during the growing season, the more nutritious and digestible young forbs and leaves of shrubs form a substantial part of bison diets (Bergmann et al. 2015, Craine et al. 2015, Leonard et al. 2017). Our result that in winter, realised macronutrient niches were more constrained than in summer is not surprising because, throughout North America, bison are limited to consuming standing dead vegetation, primarily graminoids, during the non-growing season. We limited our winter investigation to January to March, because data for bison diets in late autumn and early winter were limited. We suggest that researchers should consider the early winter diets of bison, as the few studies that do report bison diets in October to

Table 2. Summary of compositional linear models used to investigate the environmental and climactic factors influencing America bison's *Bison bison* food exploitation and realised macronutrient niches. Bold *P* values indicate significant or marginally significant coefficients in the model. The models were generated using isometric log-ratios of the percentage of forage groups and macronutrients in each herd's diet as the response variables. We have back-transformed the coefficients calculated in the compositional linear models so that the coefficients reported here can be interpreted as the amount of change in the ratio of the forage groups or macronutrient per one unit change in the predictor variable. Compositional linear models were analysed for annual and seasonal (i.e., growing and non-growing seasons) diets. Note that for annual and growing season diets a quadratic term was used for latitude in the percent forb:graminoid models due to the spread of the data. For brevity, we abbreviated graminoids (G), browse (B), forbs (F), carbohydrates (C), proteins (P), and lipids (L).

Annual			Growing season			Non-growing season		
B:G	Estimate	*P*	B:G	Estimate	*P*	B:G	Estimate	*P*
Latitude	1.23	**0.006**	Latitude	1.07	0.481	Latitude	1.17	**0.051**
Elevation	1.00	0.141	Elevation	1.00	0.756	Elevation	1.00	0.346
Precipitation	1.06	0.231	Precipitation	1.01	0.817	Precipitation	0.97	0.436
F:G	Estimate	*P*	F:G	Estimate	*P*	F:G	Estimate	*P*
Latitude^2	1.01	0.269	Latitude^2	0.94	0.299	Latitude	0.81	0.803
Elevation	1.00	0.277	Elevation	1.00	0.276	Elevation	1.00	0.286
Precipitation	1.03	0.338	Precipitation	1.03	0.641	Precipitation	0.90	0.233
P:C	Estimate	*P*	P:C	Estimate	*P*	P:C	Estimate	*P*
Latitude	1.01	0.456	Latitude	1.02	0.811	Latitude	1.02	0.973
Elevation	1.00	0.197	Elevation	1.00	0.466	Elevation	1.00	0.740
Precipitation	1.00	0.187	Precipitation	1.00	0.977	Precipitation	1.00	0.924
L:C	Estimate	*P*	L:C	Estimate	*P*	L:C	Estimate	*P*
Latitude	1.02	**0.016**	Latitude	1.02	**0.003**	Latitude	1.02	**0.066**
Elevation	1.00	0.838	Elevation	1.00	0.237	Elevation	1.00	0.781
Precipitation	1.00	0.981	Precipitation	1.00	0.284	Precipitation	1.00	0.906

December describe higher levels of consumption of unusual forage items, such as lichens and horsetails *Equisetum* spp. (Larter & Gates 1991, Larter & Allaire 2007). Bison could be foraging more intensively on these items in order to build up reserves of particular minerals and micronutrients. For example, *Equisetum* spp. are known to have high levels of cations, which are vital for metabolic processes such as the active movement of molecules across tissue membranes (van Soest 1982).

We found that bison diets significantly increased in the percentage of lipids relative to carbohydrates as latitude (in °N) increased. A study of European omnivores suggested that carnivory (and, by extension, the percentages of lipids and protein in the diet) increases with latitude (Vulla et al. 2009). However, other studies have suggested that spatially explicit environmental factors explain dietary patterns better than latitude (Gaston et al. 2008). It is possible that the higher consumption of lipids by bison at higher latitudes could be a mechanism contributing to the pattern described by Bergmann's rule: body size tends to increase with increasing latitude or decreasing temperatures (Bergmann 1847, Mayr 1956). Studies on endotherms show that 70% of taxa follow Bergmann's rule,

but the mechanisms that drive this trend are still poorly understood (Millien et al. 2006, Ho et al. 2010). A higher percentage of dietary lipids is likely to be of benefit to animals inhabiting cold climates, because lipids contribute more to stored energy and fat reserves than both carbohydrates and protein (van Soest 1982). We found that browse items were the greatest contributor of lipids in bison diets. With the increased intake of browse, there is a corresponding increase in lipid consumption, which may lead to greater fat reserves and overall mass, both of which are necessary for survival in the boreal north. However, we acknowledge that our study specifically examines the percentages of macronutrients in bison diets and that the amount of food consumed is also a critical aspect of building fat reserves. During the growing season in particular, bison require large amounts of lipid. Parturition occurs early in the growing season and lactation results in the highest lipid demands for bison throughout the year (Hudson & White 1985). Further, bison enter a slump in body weight during winter, due to reduced availability of forage and lower metabolic rates, making survival dependent on their ability to gain adequate mass during the growing season (Parker et al. 2009, Huntington et al.
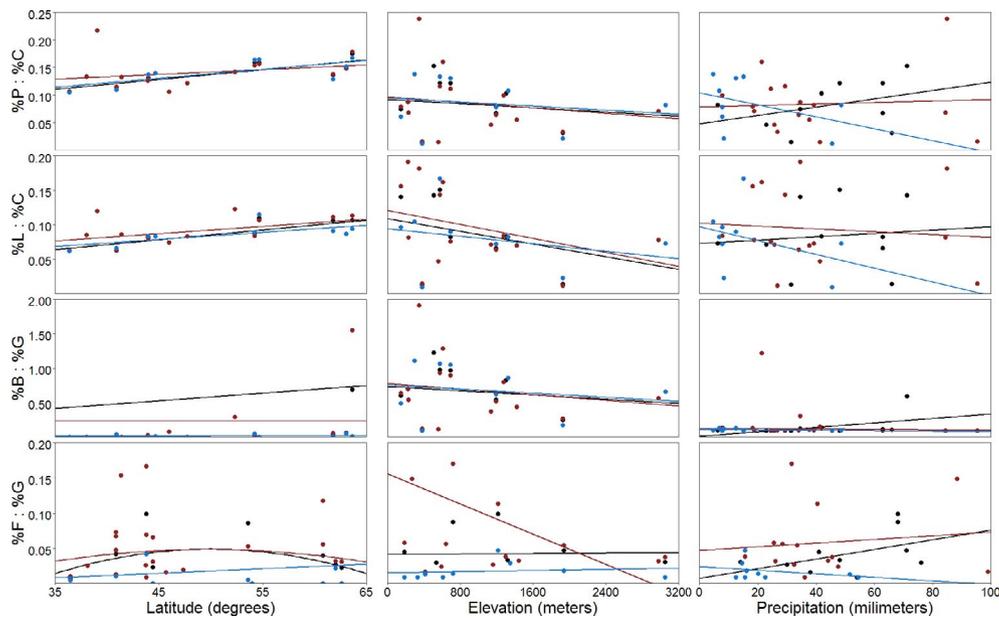
Fig. 7. Linear and quadratic relationships between ratios of proteins (P) to carbohydrates (C), lipids (L) to carbohydrates, browse (B) to graminoids (G), and forbs (F) to graminoids and the predictors (latitude, elevation, and precipitation) used in regression models. Points represent individual herds, with circles and solid lines representing annual diets, squares and dashed lines representing growing season diets, and triangles and dotted lines representing non-growing season diets. For annual and growing season diets, a quadratic term was used for latitude in the percentage forbs:graminoid models due to the spread of the data.

2019). During mating, in July or August, females have their highest fat content and spend their time foraging on high-quality items, whereas males spend less time foraging and more time tending to females (Cunfer & Waiser 2016). Dietary protein is also important for lean mass deposition and skeletal growth (Frandsen et al. 1954, Solon-Biet et al. 2014). The higher percentages of protein and lipid we found in the diets of more northerly wood bison are consistent with the suggestion that bison diets are of higher quality in cooler and wetter regions (Jorns et al. 2019). While we did not explicitly test for differences in available forage, the higher percentage of browse in boreal forests than in the great plains is likely to contribute to observed differences in browse and macronutrient content in bison diets. We would like to encourage those studying animal diets to report the availability of food items if possible, as only three out of the 26 studies we reviewed reported data on forage availability.

Recent bison dietary studies have documented a difference between functional forage groups identified in the diet dependent on the method of diet analysis used (e.g. Craine et al. 2015). DNA barcoding of the diet suggests that bison consume more forbs than commonly identified in other studies (Fig. 6). DNA barcoding is considered to be less biased towards less easily digestible plant materials (e.g. graminoids) than other methods, such as microhistology (Varva & Holechek 1980, Garnick et al. 2018). Despite the difference in diet composition, there appears

to be little difference in the percentages of macronutrient in diets estimated using different methods (Fig. 6). Assuming the diets were estimated accurately for each method, the difference may mean that bison regulate their diet towards a preferred dietary intake of macronutrients, despite differences in the types of forage groups consumed. Where there are true differences in the percentage of food group estimates within diets between methods of analysis, the consistent percentages of estimated macronutrients found across methods suggest that such analytical differences may have little or no effect on the nutritional estimates of bison diets.

Wood bison and plains bison have long been considered unique subspecies of the American bison, although genetic evidence suggests that all extant herds now classed as wood bison share a genetic association with both subspecies (Ball et al. 2016). Size, hump position, and fur colour are the primary characteristics used to distinguish the two subspecies (van Zyll de Jong et al. 1995). We suggest that future research should consider the potential relationship between phenotypic traits and the diets and nutrition of bison herds. We posit that this information is important for researchers and managers considering translocation or reintroduction of bison in the north. Future researchers should investigate which shrub and tree species bison are selecting, and what macronutrient content these forage items offer, in order to inform managers in more detail about the bison's dietary preferences.

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