Dietary Macronutrient Profiles of Free-Ranging European Brown Bears Differ Between Climate Regions

Journal of Animal Physiology and Animal Nutrition

Verbist, Leen; De Cuyper, Annelies; Bosch, Guido; Zedrosser, Andreas; Coppens, Violette et al

https://doi.org/10.1111/jpn.14125

Journal of Animal Physiology and Animal Nutrition

WILEY

Journal of Animal Physiology and Animal Nutrition

ORIGINAL ARTICLE

Zoo Animals and Exotics

Dietary Macronutrient Profiles of Free-Ranging European Brown Bears Differ Between Climate Regions

Leen Verbist[1] | Annelies De Cuyper[2] | Guido Bosch[3] | Andreas Zedrosser[4,5] | Violette Coppens[6] | Sarah Depauw[1]

[1]Agro-Bio Research Group SALTO, Agro- and Biotechnology, Odisee University of Applied Sciences, Sint-Niklaas, Belgium | [2]Department of Veterinary and Biosciences, Faculty of Veterinary Medicine, Ghent University, Merelbeke, Belgium | [3]Animal Nutrition Group, Department of Animal Sciences, Wageningen University & Research, Wageningen, The Netherlands | [4]Department of Natural Sciences and Environmental Health, University of South-Eastern Norway, Bø i Telemark, Norway | [5]Department of Integrative Biology and Biodiversity Research, Institute of Wildlife Biology and Game Management, University of Natural Resources and Life Sciences, Vienna (BOKU), Vienna, Austria | [6]Collaborative Antwerp Psychiatric Research Institute, Faculty of Medicine and Health Sciences, University of Antwerp, Antwerp, Belgium

Correspondence: Leen Verbist (leen.verbist@odisee.be)

Received: 8 January 2025 | **Revised:** 26 March 2025 | **Accepted:** 15 April 2025

Keywords: climate | diet | Europe | nutrient | Ursid

ABSTRACT

Whether climate region affects macronutrient intake in species is unknown. Because of their wide variety of habitats with varying environmental conditions and local food availability, the free-ranging European brown bear was used as a model species to study the dietary macronutrient profile in relation to climate region (using the Köppen-Geiger climate classification system), season and supplemental feeding of anthropogenic foods. Climates included were cold (regions in Norway, Sweden, Estonia and Slovakia), temperate (regions in Slovenia and Spain) and warm (regions in Croatia and Greece). Regardless of climate region, protein content was higher, and carbohydrate content was lower in spring and summer diets compared to autumn and winter diets. Diets in warm climate regions were marked by a high (digestible) carbohydrate content compared to cold climates and a low protein content compared to cold and temperate climates. A low protein to non-protein ratio, close to the optimum reported for brown bears (0.2 ME basis), was found in autumn in every climate type, and was present all year round in warm climates. At supplemented feeding sites, high (digestible) carbohydrate and low protein contents were observed compared to natural feeding sites. Supplementation also decreased seasonal variation in macronutrient composition. Fat content did not vary across seasons, climate type or with supplemental feeding. Fibre contents varied with season, climate type and supplemental feeding; however, differences were very small. Although seasonal fluctuations of macronutrients follow similar patterns across climate regions, macronutrient profiles differ between climate regions, corroborating that external conditions can influence macronutrient balance in species.

1 | Introduction

The macronutrient balance (i.e., the proportions of protein, fat, and carbohydrates) of a diet is important for physiological functions such as growth, reproduction and immune functions (Simpson et al. 2004; Cotter et al. 2011; Jensen et al. 2012; Erlenbach et al. 2014) and therefore plays a key role in shaping a species' foraging behaviour. The effects of climate on a species' macronutrient balance are poorly understood. Interactions of climate with a species' foraging behavior are typically studied in terms of dietary ingredients or energy intake (e.g., Tremblay and Cherel 2003; Zalewski 2005; Zhou et al. 2011; Bojarska and Selva 2012; Papakosta et al. 2014), but only few studies have expanded their findings into the corresponding macronutrient intake of a species. For example, although dietary ingredient composition is affected by climate region, similar macronutrient composition across climate regions has been found in European pine martens (*Martes martes*) (Remonti et al. 2016) and Eastern gorillas (*Gorilla beringei*) (Rothman et al. 2007). In contrast, the dietary ingredient and thereby also the macronutrient composition differs in relation to climate regions in the wild boar (*Sus scrofa*) (Senior et al. 2016). Species that occupy a broad geographic range, in which environmental conditions can vary considerably (Bojarska and Selva 2012), therefore lend themselves to studying the effects of climate on macronutrient balance.

Brown bears (*Ursus arctos)* occupy a wide variety of habitats and climate regions (Bojarska and Selva 2012) which is reflected in their extremely broad dietary range (Bojarska and Selva 2012; Mateo Sánchez et al. 2014; Hilderbrand et al. 2018, 2019). Brown bears are generalist omnivores and have highly flexible diets that are strongly influenced by locally and seasonally available foods (Kavčič et al. 2015; Stenset et al. 2016; Denny et al. 2018; Hilderbrand et al. 2018), which results in large interpopulation diet differences (Bojarska and Selva 2012; Coogan et al. 2014, 2018; López-Alfaro et al. 2015).

The macronutrient composition (i.e., protein, carbohydrates, fat) of brown bear diets in many populations generally is dominated by protein in the spring and early summer and carbohydrates in autumn (Coogan et al. 2018). Bears hibernate during the winter months, a physiological and behavioral adaptation that allows them to survive harsh environmental conditions (López-Alfaro et al. 2013; Delgado et al. 2018). The fat reserves obtained during hyperphagia, a period of excessive eating during the summer and autumn months, are their main sources of energy during hibernation (Barboza et al. 1997). A self-selection study with captive brown bears by Erlenbach et al. (2014) suggests that they prefer low-protein diets, that is, 17% protein and 83% non-protein (carbohydrates and fat) on a metabolizable energy basis, to optimize fat gain. Similarly, wild brown bears in North America were observed to ingest a mixed diet of salmon (*Oncorhynchus* spp.) and berries with a low dietary protein to non-protein ratio, even though a salmon-only diet would suggest a higher energy return (Rode et al. 2006; Robbins et al. 2007). This low protein to non-protein ratio is considered optimal for several ursid species (Rode et al. 2021; Robbins et al. 2022). However, Coogan et al. (2018) collated dietary macronutrient data of brown bears world-wide and observed considerable variation in the protein to non-protein ratio. De Cuyper et al. (2023) observed a low such ratio in the diet of Swedish brown bears but only in autumn. Bojarska and Selva (2012) suggest that climate in combination with the local food availability affect the nutritional and energetic requirements of brown bears, which in turn suggests that macronutrient balance in brown bears is a result of external rather than intrinsic processes.

Here we use the European brown bear as a model species to study the effects of climate variation on the nutritional profile of populations. Several populations of brown bears are distributed throughout Europe (Zedrosser et al. 2001; Chapron et al. 2014) with marked differences in feeding habits and denning behavior. In southern populations, bears generally rely more on vegetation, hard mast, and fruits but less on vertebrates as compared to northern populations (Cicnjak et al. 1987; Swenson, Adamič, et al. 2007; Vulla et al. 2009; Paralikidis et al. 2010; Bojarska and Selva 2012; Ciucci et al. 2014; Stenset et al. 2016). Bears in northern Europe spend up to 7.5 months in hibernation, while some individuals may not hibernate at all in southern Europe (Hissa 1997; Huber and Roth 1997; Friebe et al. 2001; Nores et al. 2010; Bogdanović et al. 2024). Based on population differences in diet composition and denning ecology, we hypothesized (1) that the seasonal macronutrient profile of brown bear populations in climate regions in Europe fluctuates according to season with protein domination in spring and early summer and carbohydrate domination in late summer and autumn; (2) nutrient profiles of European bear populations differ between climate regions, with higher protein and lower carbohydrate proportions in colder climate regions compared to warmer regions; (3) the protein to non-protein ratio varies in relation to climate regions. Coogan et al. (2018) showed that the macronutrient profile of annual diets in populations with anthropogenic supplements (from agricultural fields and supplemental feeding sites) is significantly different (high carbohydrate proportion) from those with natural foods. Starch-rich food items are often provided at supplemental feeding sites such as cereals, corn, or other carbohydrate-rich materials (fleshy fruits) [e.g., Vulla et al. (2009); Štofik et al. (2013); Kavčič et al. (2015)]. Therefore, we hypothesized that (4) populations with access to supplemental feeding sites have a higher dietary carbohydrate proportion compared to populations without access to supplemental feeding sites or field crops.

2 | Methods

2.1 | Literature Survey

All data were collected between June 2018 and February 2023 through multidisciplinary search engines Web of Science and Google Scholar. In addition, reference and citation tracking was used to expand the scope of the search and to identify the original resources whenever possible. This study focused exclusively on brown bear populations in study locations on the European continent. The studies used were based on fecal analysis and have identified the food items on the basis of bones, exoskeletons, seeds, or cellular characteristics of plants that were not digested (Trites and Joy 2005). Studies were only selected when calendar years were subdivided into seasonal periods based on geo-biological phenomena such as food abundance and changes in nutrient availability, to compare different spatial ecological data sets. Note that several papers describing the diets of free-ranging European brown bears (e.g., Elgmork and Kaasa 1992; Naves et al. 2006) were not included in our study because the subdivisions of the data into time periods (e.g., division in three bear phenological periods) made comparison not possible. Generally, the time periods used in our study were defined as spring (March–May), summer (May–August), fall (September–November), and winter (December–March) (Cicnjak et al. 1987; Clevenger et al. 1992; Dahle et al. 1998; Persson et al. 2001; Vulla et al. 2009; Paralikidis et al. 2010; Štofik et al. 2013; Kavčič et al. 2015; Stenset et al. 2016). Supplemental feeding was defined as the intentional supplementation of anthropogenic foods, such as cereals (e.g., maize (*Zea mais*)) and livestock carrion, for use by wild animals for conservation or hunting purposes at multiple feeding sites (Selva et al. 2014; Kavčič et al. 2015).

2.2 | Subdivision Into Climate Regions

The study sites of the eligible studies in Europe and their associated macronutrient data were divided into climate regions based on the Köppen-Geiger climate classification system (Beck et al. 2018). This system describes the global distribution of biomes based on seasonality and on threshold values of monthly air temperature and precipitation, with different regions in a similar class having common vegetation characteristics (Beck et al. 2018). The Köppen–Geiger climate classification system is widely used in studies on climate and climate change, hydrology, or physical geography (Kottek et al. 2006). Climate variables are the predominant factors influencing the distribution of species at large spatial scales (Peel et al. 2007; Beck et al. 2018). The Köppen–Geiger climate classification distinguishes between five zones, that is, the equatorial zone (A), arid zone (B), warm temperate zone (C), snow zone (D), and the polar zone (E) (Table 1). The second letter in a zone identification indicates the amount of precipitation (f, m, w, W, s, S, T; see Beck et al. (2018) for precipitation range criteria), and the third letter indicates air temperature (a, b, c, d, h, k; see Beck et al. (2018) for temperature range criteria) (Peel et al. 2007; Beck et al. 2018) (Table 1). Some study areas were spread over two Köppen-Geiger climate zones resulting in the aggregation of both climate zones (e.g. Nord-Trøndelag, Norway: Dfb/Dfc). See Table 1 for an overview of study areas and associated climate(s) zones. Climate regions were further divided into climate types (cold (all 'D' zones), temperate ('C' zones with 'b' temperature (warm summer)), and warm ('C' zones with 'a' temperature (hot summer)) for statistical purposes (Table 1).

2.3 | Food Item Composition of Brown Bear Diets

The fecal volume (FV, %) of food items was extracted from all eligible studies and food items were defined to the lowest taxonomic level possible. Subsequently, all items in the brown bear diet were divided into eight food categories: Hard mast (e.g., acorns), soft mast (e.g., berries), green vegetation (e.g., grasses, herbs), cereals (agricultural crops/cultivated plants), vertebrates, invertebrates (insects), fungi (fungi/mushrooms), and other (e.g., pebbles, unidentifiable items). In the category cereals, we attempted to differentiate between cereals provided at feeding sites and cereals foraged in agricultural fields based on the information provided in the papers. In these studies, cereals had been seperated by their origin from either supplemental feeding sites or as part of the green vegetation category which indicates that bears foraged in agricultural fields. The categories "other" and "fungi" were not included in macronutrient calculations due to their limited contribution to the diet.

To account for the digestion bias inherent to FV (Hewitt and Robbins 1996), an approximation of the original diet's composition was made by calculating the estimated dietary content (EDC, %). The estimates of FVs in the eligible studies were multiplied by correction factors (Table 2), extracted from Hewitt and Robbins (1996) and Bojarska and Selva (2013), or derived from other studies using correction factors (Dahle et al. 1998; Persson et al. 2001; Ciucci et al. 2014; Kavčič et al. 2015). The percentual composition of a diet was calculated as:

$$\mathrm{EDC}(\%) = \frac{\text{Correction factor (food item)} * \text{FV (food item)}}{\sum(\text{Correction factor} * \text{FV}) \text{ for all food items}} * 100$$

We directly extracted the EDC values without any further adjustment from studies with existing EDC calculations. See Supporting Information File S1 for the EDC of the major food categories per season and climate regions.

2.4 | Macronutrient Composition of European Brown Bear Diets

To approximate the macronutrient composition of the brown bear diet in each climate region, we extracted the dry matter (DM), crude protein (CP), ether extract (EE), ash, crude fibre (CF), total dietary fibre (TDF), and nitrogen-free extract (NfE) of each food item from the literature (Cicnjak et al. 1987; Kuhnlein 2002; Barros et al. 2010; Schwarm et al. 2010; Fowler 2011; Plantinga et al. 2011; NRC 2012; Bosch et al. 2015). When the composition of a food item could not be found, data from a similar food item or an average of several similar food items (same genus) were used. When the percentage of only the food category was available and no further specification of the food items within that category was given, we used the median nutrient composition of all known food items in this food category from the entire data set. If NfE was not available, but data on CP, EE, Ash, and CF were available, NfE on DM basis was determined by by 100 – CP – EE – CF – Ash. As suggested by Clauss et al. (2010), an estimation of NfE was computed using TDF instead of CF values if data for CF were not available. The macronutrient concentration in the diet (% DM) was calculated as:

$$\text{Macronutrient } (\%DM) = \sum \mathrm{EDC}_{\text{food item}} \times \text{macronutrient concentration}_{\text{food item}}$$

Modified Atwater factors (kJ/100 g) (NRC 2006) were used to calculate the dietary ME (kJ/100 g DM) content:

$$\mathrm{ME} = 16.74 \times \mathrm{CP} + 37.66 \times \mathrm{EE} + 16.74 \times \mathrm{NfE}$$

with CP, EE, and NfE on a % of DM basis.

The CP, EE, and NfE content were additionally expressed on a ME basis by dividing the ME contribution of every nutrient (i.e.,16.74 × CP, 37.66 × EE or 16.74 × NfE) by the total ME. The nutrient composition on ME basis was then used to calculate the protein to non-protein ratio as CP:(EE+NfE). See Supporting Information File S1 for the nutrient composition per season and climate region.

2.5 | Data Compilation and Statistics

All EDC values below the detection limit were given an arbitrary value of 0.1%. which can result in a minor over/underestimation of a food category. All food items measured but not found in the feces were scored as 0%, and all missing values were excluded. For each study site, the following data were extracted: country, Köppen–Geiger climate classification (climate region), climate

TABLE 1 | Location of study sites with the number of faecal samples collected from European brown bears per studied season and the climate classification per study site according to the definitions by Köppen–Geiger as well as the climate and feeding type division per study site.

Site	Seasons	Samples	Climate classification[k,l]	Climate type	Feeding type
Pasvik Valley, Norway[a]	Spring	$n = 35$	Subarctic (Dfc)	Cold	Natural
	Summer	$n = 49$			
	Autumn	$n = 35$			
Nord-Trøndelag, Norway[b]	Spring	$n = 28$	Warm-summer humid continental/subarctic (Dfb/Dfc)	Cold	Natural
	Summer	$n = 58$			
	Autumn	$n = 32$			
Dalarna & Gävleborg, Sweden[b]	Spring	$n = 25$	Warm-summer humid continental/subarctic (Dfb/Dfc)	Cold	Natural
	Summer	$n = 52$			
	Autumn	$n = 71$			
Jämtland, Sweden[c]	Spring	$n = 141$	Warm-summer humid continental/subarctic (Dfb/Dfc)	Cold	Natural
	Summer	$n = 93$			
	Autumn	$n = 305$			
Lääne-Virumaa, Ida-Virumaa & Jõgevamaa, Estonia[d]	Spring	$n = 16$	Warm-summer humid continental (Dfb)	Cold	Supplemental
	Summer	$n = 20$			
	Autumn	$n = 106$			
Poloniny National Park, Slovakia[e]	Spring	$n = 35$	Warm-summer humid continental (Dfb)	Cold	Supplemental
	Summer	$n = 25$			
	Autumn	$n = 97$			
	Winter	$n = 58$			
Pol'ana, Slovakia[f]	Spring	$n = 62$	Warm-summer humid continental (Dfb)	Cold	Supplemental
	Summer	$n = 78$			
	Autumn	$n = 87$			
	Winter	$n = 16$			
Plitvice Lakes, Croatia[g]	Spring	$n = 18$	Humid subtropical (Cfa)	Warm	Natural
	Summer	$n = 10$			
	Autumn	$n = 55$			
	Winter	$n = 12$			
Grevena prefecture, Greece[h]	Spring	$n = 142$	Humid subtropical/hot-summer Mediterranean (Cfa/Csa)	Warm	Natural
	Summer	$n = 114$			
	Autumn	$n = 104$			
Snežnik, Menišija & Kočevsko, Slovenia[i]	Spring	$n = 75$	Temperate oceanic (Cfb)	Temperate	Supplemental
	Summer	$n = 119$			
	Autumn	$n = 169$			

(Continues)

TABLE 1 | (Continued)

Site	Seasons	Samples	Climate classification[k,l]	Climate type	Feeding type
Cantabrian Mountains, Spain[j]	Spring	$n = 341$	Temperate oceanic (Cfb)	Temperate	Natural
	Summer	$n = 104$			
	Autumn	$n = 315$			
	Winter	$n = 169$			

[a](Persson et al. 2001).
[b](Dahle et al. 1998).
[c](Stenset et al. 2016).
[d](Vulla et al. 2009).
[e](Štofik et al. 2013).
[f](Skuban et al. 2016).
[g](Cicnjak et al. 1987).
[h](Paralikidis et al. 2010).
[i](Kavčič et al. 2015).
[j](Clevenger et al. 1992).
[k](Arnfield 2017).
[l](Peel et al. 2007).

type (cold, temperate, warm), season (spring, summer, autumn, winter), feeding type (natural or supplemental feeding), the food item composition (EDC) and the nutrient composition on both DM and ME basis. Only a few studies described the food composition in winter because it is assumed that bears hibernate during winter or because the study area was difficult to reach due to snow conditions (Paralikidis et al. 2010). No data were available for the winter season in the cold regions Dfc and Dfb/Dfc and for warm region Cfa/Csa (Table 1). Supplemental feeding sites were not present in the warm regions (Table 1).

All statistical analyses were performed with SPSS version 28 with a significance level of $p < 0.05$. A univariate general linear model was used to test the effects of the independent variables climate type (cold, temperate and warm), season (spring, summer, autumn, winter), and feeding type (natural, supplemental feeding) as well as their two-way interactions on the following dependent variables: (1) CP (%DM), (2) CF (%DM), (3) EE (%DM), (4) NfE (%DM), (5) ME (kJ/100 g DM), (6) CP (%ME), (7) EE (%ME), (8) NfE (%ME), and (9) the CP:(EE+NfE) ratio (on ME basis). Interactions were removed from the model when not significant. Post hoc comparisons were done using a Tukey's test. Visual inspection of residual plots (residual vs fitted plots, normal Q-Q plots and histograms) indicated normality of model residuals.

3 | Results

A total of 10 diet studies from 11 different bear populations across Europe were selected based on the predetermined criteria (Table 1). Seven sites were in the cold climate type ($n = 1$ for Dfc, $n = 3$ for Dfb/Dfc, and $n = 3$ for Dfb), two in the temperate climate type (Cfb), and two in the warm climate type (Cfa and Cfa/Csa). Supplemental feeding was practiced at the study sites of Snežnik, Menišija & Kočevsko (Slovenia; Cfb), Lääne-Virumaa, Ida-Virumaa & Jõgevamaa (Estonia; Dfb), Poloniny National Park (Slovakia; Dfb), and Pol'ana (Slovakia; Dfb) (Table 1).

The dietary CP percentage (on dry matter basis) in all climates and feeding types was higher in spring and summer compared to autumn and winter ($p < 0.001$) (Figure 1 and Table 3). In cold and temperate climates, the CP percentage was generally higher than in warm climates ($p < 0.001$) and overall, CP percentage of diets was higher in natural compared to supplemental feeding sites ($p < 0.001$) (Table 3). There was no overall seasonal, climate or feeding type effect on the dietary EE percentage. The NfE percentage was lowest in spring and summer compared to autumn ($p < 0.001$). Warm climates were marked by a significant higher NfE percentage compared to cold climates ($p < 0.001$) and in supplemental feeding sites, the dietary NfE percentage was generally higher than in natural feeding sites ($p < 0.001$) (Table 3). The dietary fibre percentage differed between seasons ($p = 0.038$) with spring and winter having slightly higher levels than summer and autumn (although adjusted post hoc p-values were not significant). The fibre percentage was higher in warm compared to cold climates ($p = 0.022$). In spring and summer, the fibre percentage was higher in warm (18.2 ± 4.4 SD, 11.4 ± 7.1 SD, resp.) compared to cold (6.8 ± 6.6 SD, 4.3 ± 2.3 SD, resp.) and temperate climates (9.0 ± 0.72 SD, 5.0 ± 1.7 SD, resp.) but in autumn and winter, the dietary fibre percentage was higher in cold (6.2 ± 2.6 SD, 11.2 ± 1.1 SD, resp.) and temperate climates (7.1 ± 1.0 SD, 11.3 ± 0 SD, resp.) than in warm climates (5.7 ± 0.0025 SD, 5.04 ± 0 SD, resp.) ($p = 0.036$). In supplemental feeding sites, the dietary fibre percentage was higher than in natural feeding sites ($p = 0.022$) (Table 3).

Cold climate diets had a higher ME content than warm climate diets ($p = 0.007$) (Figure 2 and Table 3). All macronutrient percentage on ME basis followed the same fluctuations per season, climate and feeding type as on a DM basis ($p < 0.01$) (Figure 3 and Table 3) except for NfE, where warm climates were marked by a significant higher NfE percentage compared to cold climates but also temperate climates ($p < 0.001$) (Figure 3 and Table 3). The dietary protein to non-protein ratio (ME basis) was higher in spring and summer diets compared to autumn and winter diets ($p < 0.001$) and higher in cold and temperate regions than in warm regions ($p < 0.001$). Supplemental feeding sites were marked by a lower ratio compared to natural feeding sites ($p < 0.001$) (Figure 3 and Table 3).

TABLE 2 | Food items and their respective correction factors (dry mass ingested (g)/residual volume (mL) in faeces).

Food item	Correction factor
Hard mast	
Quercus sp.	1.50[a]
Fagus sylvatica	1.18[b]
Corylus avellane	1.58[b]
Soft mast	
Sorbus sp.	0.93[a]
Rosa Canina	0.93[a]
Rubus fruticose	0.87[a]
Ilex aquifolium	0.93[a]
Vaccinium sp.	0.54[a]
Crataegus monogyna	0.93[a]
Empetrum sp.	0.54[c,d,e]
Rhamnus alpinus	1.08[f]
Malus sp.	0.51[a]
Green vegetation	
Cryptogams	0.26[a]
Graminoids	0.26[a]
Forbs	0.26[a]
Ferns	0.26[a]
Horsetails	0.16[a]
Herbaceous plants	0.26[a]
Sprouts	0.26[a]
Fungi	0.26[a]
Shrub material	0.26[a]
Other plant items	0.26[a]
Vertebrates	
Unknown/carrion	2.00[d,e,g]
Horses	3.00[f]
Cattle	3.00[f]
Sheep	3.00[f]
Goats	1.50[f,g]
Cervus elaphus	1.50[f,g]
Capreolus capreolus	1.50[f,g]
Small mammals	4.00[a]
Invertebrates	
Unknown	1.10[a]
Formica v.	1.10[a]
Camponotus herculeanus	1.10[a]
Formicidae	1.10[a]
Apidae	1.10[a]
Coleoptera	1.10[a]
Egg/larvaes	1.10[a]

[a](Hewitt and Robbins 1996).
[b](Bojarska and Selva 2013).
[c](Dahle et al. 1998).
[d](Persson et al. 2001).
[e](Stenset et al. 2016).
[f](Ciucci et al. 2014).
[g](Kavčič et al. 2015).

4 | Discussion

Macronutrient profiles of European brown bear diets vary with season, with climate type, and with the presence of supplemental feeding. The previously described seasonal pattern of protein domination in spring and summer diets and carbohydrate domination in autumn diets in many brown bear populations (Coogan et al. 2018; De Cuyper et al. 2023), is supported by our results (support hypothesis 1). Bear populations in Europe, however, can be distinct in their overall annual resource use, with one of the most pronounced differences between northern/colder and southern/warmer regions. This suggests that brown bears in Europe do not attempt to combine different food items to arrive at a species-specific nutrient proportion goal (Simpson et al. 2004; Raubenheimer et al. 2009) (no support hypothesis 2). The dietary protein to non-protein ratio was always lowest in autumn and winter compared to spring and summer, which is in agreement with recent findings that a low dietary protein to non-protein ratio (Erlenbach et al. 2014; Robbins et al. 2022) is optimal for fattening before hibernation (support hypothesis 3). European bear populations that were supplemented with anthropogenic foods (mainly cereals) had higher percentages of carbohydrates and lower percentages of protein in their diet compared to natural environments. This observation is in accordance with previous results on brown bear diets that generally the carbohydrate percentage increases with the level of anthropogenic foods (Coogan et al. 2018) (support hypothesis 4).

4.1 | Macronutrient Profiles in the Active Phase in Different Climate Regions

In this study, bears living in a humid continental climate characterised by cold winters (Dfc, Dfb/Dfc) consume a large amount of animal material, particularly in spring and summer (Dahle et al. 1998; Persson et al. 2001; Stenset et al. 2016), which is reflected in a high dietary protein percentage (Supporting Information File S1; Figures 1 and 3). The research areas in the Dfc and Dfb/Dfc climate region represent a boreal forest biome (Bonan and Shugart 1989; DeAngelis 2019). Although the biodiversity in the boreal forest is less diverse compared to forests in most temperate climate regions, moose (*Alces alces*) and other ungulates are frequent in

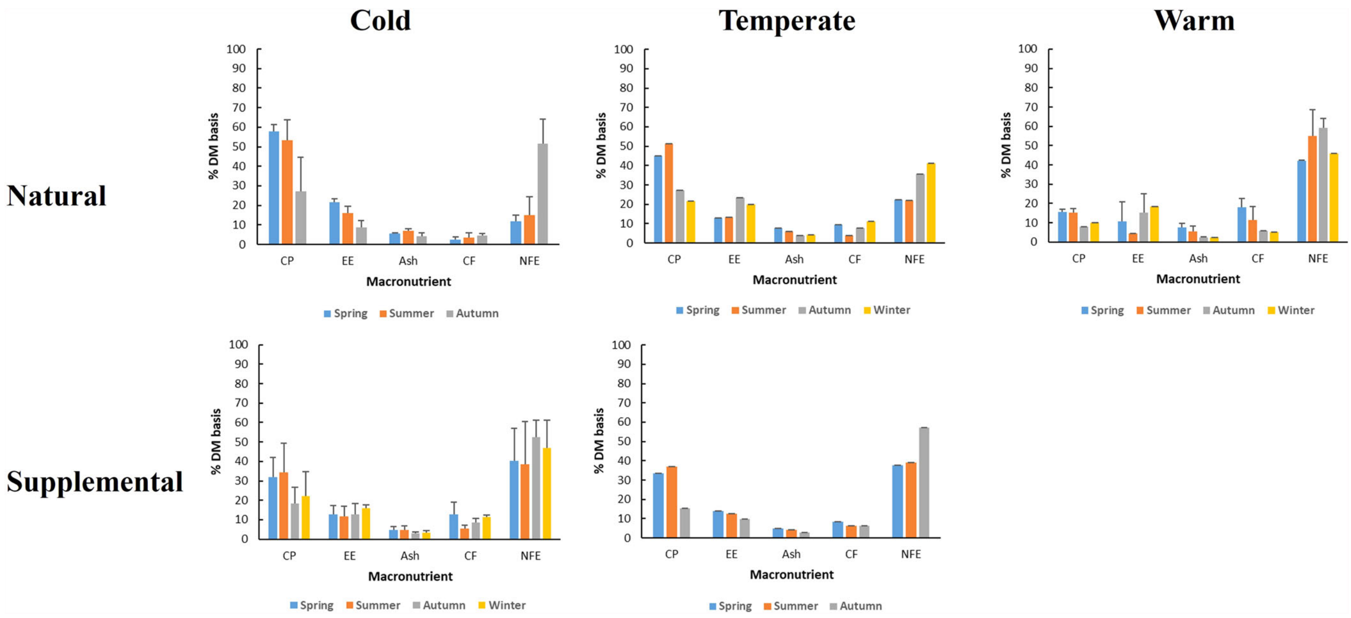

FIGURE 1 | Seasonal macronutrient composition of European brown bear diets on dry matter basis per feeding and climate type. CF, crude fibre; CP, crude protein; EE, ether extract; NfE, nitrogen-free extract. [Color figure can be viewed at wileyonlinelibrary.com]

this area (Persson et al. 2001; DeAngelis 2019). In early summer, ungulate calves become available (Ballard et al. 1981; Linnell et al. 1995; Swenson, Dahle, et al. 2007; Niedziałkowska et al. 2019). The invertebrate content is low in the Dfc climate region in comparison with bears living in the areas with a Dfb/Dfc climate (Supporting Information File S1). Invertebrates such as ants are an important source of nutrients for bears living in the boreal forest, although some authors suggest that the extent to which these foods are consumed probably depends on the availability of other nutritious food items such as ungulates (Swenson et al. 1999).

A high-protein diet is suggested to be less important for brown bears living in warm climates since these bears have a considerably shorter hibernation (Swenson, Adamič, et al. 2007; Vulla et al. 2009; Bojarska and Selva 2012). They spend an average of 2.9 months denning in winter; however, some of them awaken for short periods of time and some of them do not go into hibernation at all (Huber and Roth 1997; Nores et al. 2010; Bogdanović et al. 2024). These bears lose less muscle mass during hibernation, so that they do not have to rebuild it in spring. Therefore, their post-winter dormancy diet can be less protein-rich (Swenson, Adamič, et al. 2007; Vulla et al. 2009; Bojarska and Selva 2012). Brown bears in warm climates consumed high percentages of green vegetation mostly in spring when plants are higher in CP and have the highest protein digestibility (Mealey 1980; Cicnjak et al. 1987) (Supporting Information File S1). The natural diet in warm climates predominantly contained soft and hard mast next to green vegetation, which was reflected in high NfE percentages. The consumption of green vegetation stayed high until summer in the Cfa climate region and was gradually replaced by soft mast, which occurred earlier in Cfa/Csa regions (Supporting Information File S1). The mean fibre content in bear diets (% on DM basis) was significantly higher in warmer climates compared to cold climates although differences were small. The heavy reliance on plant material in warm climates can explain higher percentages of fibre, although this interpretation warrants some caution. De Cuyper et al. (2023) reported constant fibre percentages (25% on DM basis) in the diet of Swedish brown bears, which exceeds the levels observed in warm climates in this study (10.8%DM). This can be explained by the fact that De Cuyper et al. (2023) used TDF values with inclusion of animal fibre (i.e., indigestible proteinaceous substances in whole prey [Depauw et al. 2013]) instead of CF values. While CF is the oldest and probably most widely used technique for fibre analysis (Van Soest and McQueen 1973; de-Oliveira et al. 2012), it mainly captures fractions of cellulose, hemicellulose, and lignine (McDonald et al. 2011) and therefore underestimates the true dietary fibre content. TDF entails the complete indigestible residue after enzymatic digestion (Prosky et al. 1985) and could be viewed as a more complete measure of fibre. However, we were restricted to estimates of fibre percentages based on CF values because of the lack of TDF and animal fibre values for certain food items (Supporting Information File S1).

The European brown bear population in the Cfb temperate climate region inhabits the Cantabrian Mountains in Spain and has access to hard mast from mixed-deciduous temperate forests such as oak (*Quercus sp.*), beech (*Fagus sp.*) and chestnut (*Castanea sativa*), but also to fruits of subalpine shrubs such as *Vaccinium* spp. at higher altitudes (Clevenger et al. 1992). According to Naves et al. (2006), this bear population is the only population in Europe that feeds on both boreal and Mediterranean dietary items. From spring to autumn, there is a high density of wild ungulates, providing a steady supply of carrion (Clevenger et al. 1992), and predation on neonate roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*) occurs in spring and early summer (Blanco et al. 2011). Bears in this temperate area showed high protein percentages in their spring and summer diet comparable to bear diets in cold regions and higher than in warm regions (Supporting Information File S1). This is most likely due to the combination of a high abundance of green vegetation and vertebrates in the diet at that time (Supporting Information File S1).

TABLE 3 | Macronutrient composition (± SD) of bear diets per season, climate type and feeding type.

		% on DM basis					ME	% on ME basis			
		CP	EE	NfE	CF	Ash	kJ/100 g DM	CP	EE	NfE	CP/(EE + NfE)
Season											
	Spring	39.7^{a} (±17.2)	15.8^{a} (± 6.1)	28.5^{a} (±16.1)	9.3 (±7.0)	5.9^{a} (±1.6)	1735.7^{a} (±271.6)	37.2^{a} (±12.6)	33.1^{a} (±9.7)	29.7^{a} (±19.4)	0.65^{a} (±0.31)
	Summer	39.6^{a} (±17.1)	12.3^{a} (±5.2)	31.5^{a} (±19.9)	5.7 (±4.1)	5.7^{a} (±1.8)	1651.9^{a} (±190.2)	39.2^{a} (±14.8)	27.1^{a} (±9.5)	33.7^{a} (±23.7)	0.74^{a} (±0.44)
	Autumn	20.2^{b} (±12.8)	12.4^{a} (±6.3)	52.2^{b} (±10.4)	6.3 (±2.1)	3.4^{b} (±1.2)	1680.2^{a} (±195.1)	19.6^{b} (±10.6)	26.8^{a} (±11.1)	53.6^{b} (±15.4)	0.27^{b} (±0.20)
	Winter	19.0^{b} (± 9.4)	17.5^{a} (±2.1)	45.3^{ab} (±8.7)	9.7 (±3.2)	3.2^{b} (±1.0)	1732.5^{a} (±74.3)	18.2^{b} (±8.5)	38.1^{a} (±4.9)	43.8^{ab} (±9.1)	0.23^{b} (±0.13)
Climate type											
	Cold	37.1^{a} (± 17.9)	14.3^{a} (±5.4)	34.8^{a} (± 20.0)	6.3 (±4.3)	4.8^{a} (± 1.8)	1742.2^{a} (±180.2)	34.8^{a} (±15.0)	30.2^{a} (±9.1)	35.1^{a} (±22.1)	0.62^{a} (±0.40)
	Temperate	33.0^{a} (±12.7)	15.1^{a} (±4.7)	36.4^{ab} (±12.1)	7.6 (±2.5)	4.8^{a} (±1.6)	1731.5^{ab} (±113.9)	32.1^{a} (±12.9)	32.5^{a} (±8.0)	35.4^{a} (±13.0)	0.52^{a} (±0.31)
	Warm	12.6^{b} (± 4.0)	11.4^{a} (±7.9)	51.3^{b} (±9.6)	10.8 (±6.6)	4.8^{a} (±2.8)	1497.9^{b} (±264.0)	15.0^{b} (±6.9)	26.7^{a} (±15.3)	58.3^{b} (±11.7)	0.18^{b} (±0.10)
Feeding type											
	Natural	34.2^{a} (±20.4)	14.6^{a} (±6.7)	34.5^{a} (±19.5)	6.5^{a} (±5.2)	5.3^{a} (±2.0)	1697.7^{a} (±247.7)	32.6^{a} (±17.3)	31.0^{a} (±11.8)	36.5^{a} (±23.4)	0.59^{a} (±0.43)
	Supplemental	27.5^{b} (±11.5)	12.9^{a} (±3.8)	44.4^{b} (±13.9)	8.9^{b} (±3.9)	4.0^{b} (±1.4)	1687.9^{a} (±121.6)	27.1^{b} (±10.9)	28.4^{a} (±6.9)	44.6^{b} (±15.3)	0.40^{b} (±0.23)

Note: Different superscripts within a column and a factor type (Season, Climate type, Feeding type) indicate significant differences (post hoc tests adjusted for multiple comparisons). No superscripts were added in the CF column (except for Feeding type) because there was a significant interaction between Season and Climate type. We refer to the manuscript text for detailed results on this matter.
Abbreviations: CF, crude fibre; CP, crude protein; EE, ether extract; NfE, nitrogen-free extract; ME, metabolizable energy.

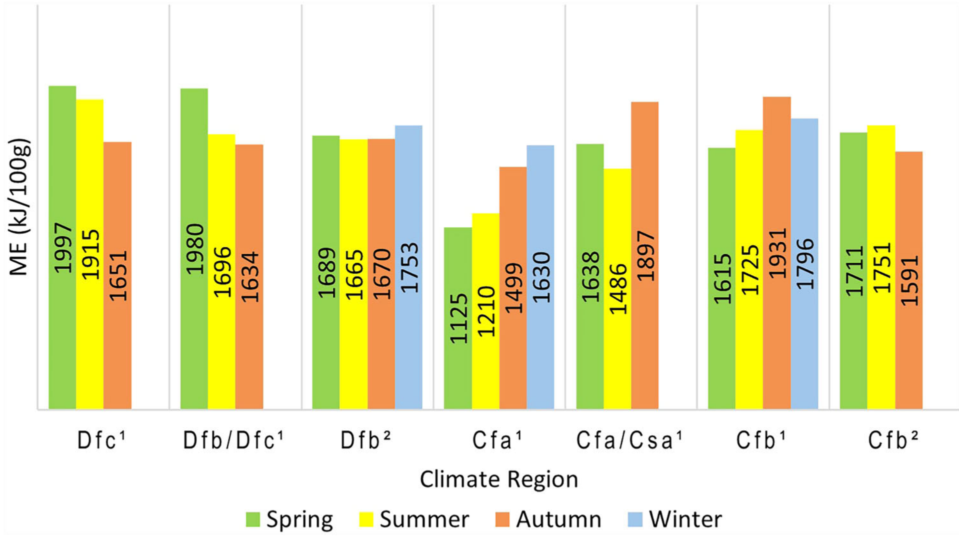

FIGURE 2 | Seasonal variation in dietary metabolizable energy content (ME kJ/100 g DM) of free-ranging European brown bears living in different climate regions. [1]Climate region with natural diets: (cold) Dfc, Pasvik Valley & Dfb/Dfc, (a) Nord-Trøndelag, (b) Dalarna & Gävleborg, (c) Jämtland; (warm) Cfa, Plitvice Lakes Nat. Park & Cfa/Csa, Grevena Prefecture; (temperate) Cfb, Cantabrian mountains. [2]Study areas with anthropogenic foods supplied at feeding sites: (cold) Dfb, (a) Lääne-Virumaa, Ida-Virumaa, Jõgevamaa, (b) Pol'ana, (c) Poloniny National Park; (temperate) Cfb, Snežnik, Menišija, Kočevsko. [Color figure can be viewed at wileyonlinelibrary.com]

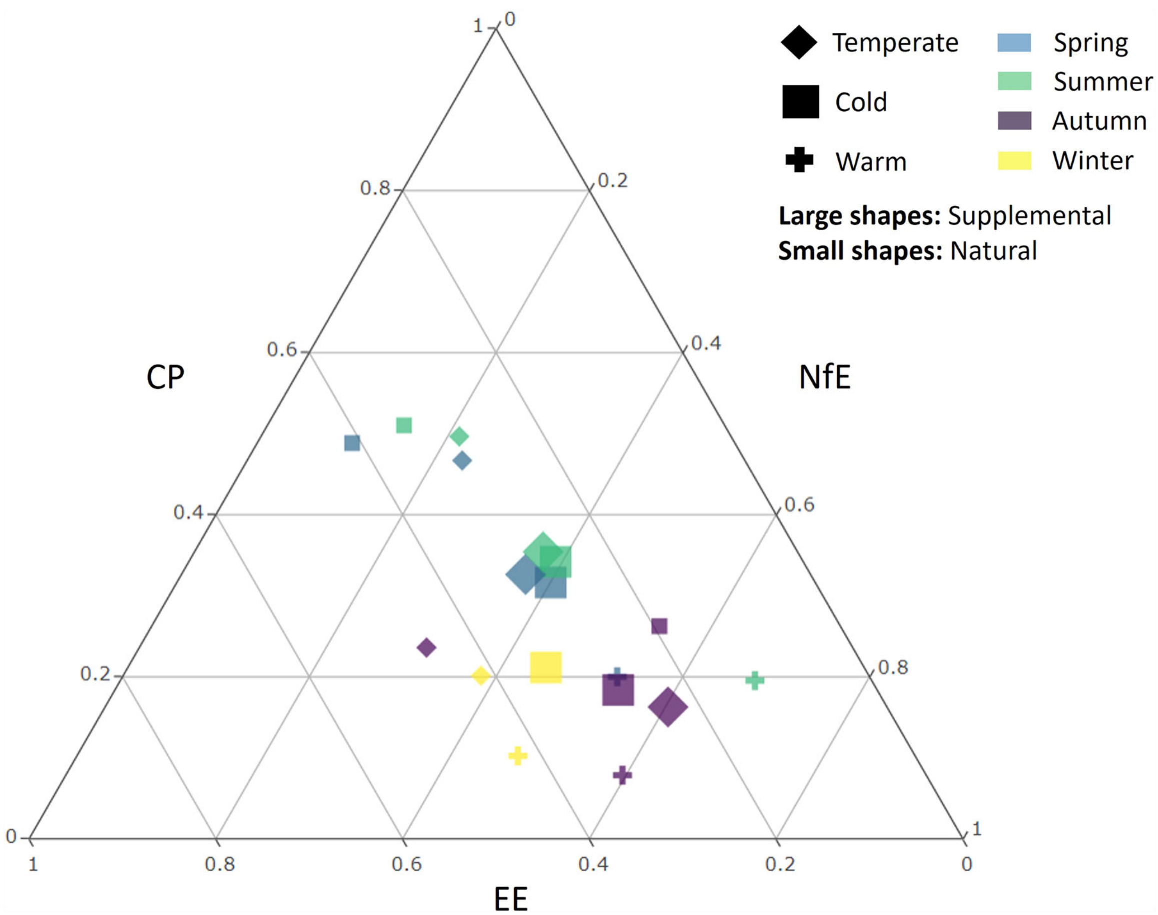

FIGURE 3 | Ternary plot of the macronutrient composition of European brown bear diets on metabolisable energy basis according to season, feeding and climate type. CP, crude protein; EE, ether extract; NfE, nitrogen-free extract. [Color figure can be viewed at wileyonlinelibrary.com]

4.2 | Macronutrient Profiles in the Pre-Denning Phase in Different Climate Regions

During hyperphagia, brown bears optimize their fat gain by targeting an optimal protein to non-protein ratio. In doing so, they appear to favour high-fat foods but can also substitute fat for carbohydrate-rich foods (Erlenbach et al. 2014). European bear populations in cold climates face limited availability of high-fat food in autumn due to the absence of hard mast trees or spawning salmon. Instead, the canopy in boreal forests in north-western Europe is dominated by tree species such as Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), birch (*Betulus spp*.), aspen (*Populus termula*) and grey alder (*Alnus incana*) (Elfström et al. 2008; Stenset et al. 2016; DeAngelis 2019). Given the scarcity of high-lipid foods within this ecosystem, these bears adopt a compensatory strategy by increasing their consumption of carbohydrate-rich soft mast sourced from the understory vegetation (Erlenbach et al. 2014). This vegetation predominantly comprises berry-bearing shrubs such as bilberry (*Vaccinium myrtillus*), crowberry (*Empetrum hermaphroditum*) and rowan (*Sorbus aucuparia*) (Elfström et al. 2008; Skuban et al. 2016; Stenset et al. 2016; DeAngelis 2019). The dietary NfE content throughout the year was significantly lower in cold climates than in warm climates, but this difference was strongly reduced during hyperphagia (Supporting Information File S1 and Figure 1).

In warm regions, hard mast such as nuts and seeds are available in the ecosystem during hyperphagia (e.g., Cicnjak et al. 1987; Supporting Information File S1) and the fat content of the diet can increase up to fivefold compared with summer (this study). The Cfa/Csa climate also contains large amounts of hard mast in the spring diet, mainly due to wintering acorns (*Quercus* spp.) leading to a relatively higher dietary fat content compared to the Cfa region. Some of the major taxa in the mixed-deciduous temperate forests include oaks (*Quercus* spp.), pines (*Pinus* spp.), hazel (*Corylus* spp.) and beech (*Fagus* spp.) (Cicnjak et al. 1987; Paralikidis et al. 2010). In addition, bears in warm regions also consume some soft mast, but less animal matter (vertebrates and invertebrates) in autumn compaired to spring and summer. The high percentage of fatty hard mast in autumn/winter diets (and also spring in the Cfa/Csa region) in warm and temperate climates did not lead to a different dietary fat content between warm, cold or temperate climates. However, the hard mast consumed across study sites in this study included *Quercus sp*., *Fagus sylvatica, Corylus sp., Juniperus communis* and *Castanea sativa*, which can vary from 1.7% to 64.6%EE on DM basis, hence depending on the proportion of the type of hard mast in the diet, this can greatly influence the fat level.

The dietary protein to non-protein ratio was lowest in autumn (and winter) compared to spring and summer in all climate types. Within the warm climate type however, the ratio was (numerically) constantly low (spring 0.25 ± 0.10 SD, summer 0.25 ± 0.083 SD, autumn 0.085 ± 0.018 SD, winter 0.11). As such, bears residing in warm climates are fitting the recent postulation that ursids are low-protein macronutrient omnivores (Rode et al. 2021; Robbins et al. 2022; Mikkelsen et al. 2024). However, our findings do not corroborate this for bears residing within cold (spring 0.75 ± 0.28 SD, summer 0.87 ± 0.45 SD, autumn 0.32 ± 0.22 SD, winter 0.28 ± 0.19 SD) or temperate regions (spring 0.68 ± 0.28 SD, summer 0.77 ± 0.31 SD, autumn 0.25 ± 0.81 SD, winter 0.25). Hence, generalizations that bears are low-protein omnivores should be interpreted with caution.

4.3 | Study Sites With Supplemental Feeding

Supplemental feeding was restricted to cold (Dfb) and temperate (Cfb) regions and led to dietary profiles that were marked by a higher carbohydrate but lower protein content compared to natural feeding sites. Coogan et al. (2018) also reported that bear diets that are rich in anthropogenic food items from agricultural fields and supplemental feeding sites have a higher carbohydrate and lower protein content compared to diets of bears living in natural areas. Brown bears in both temperate Cfb and cold Dfb regions, despite their large differences in the availability of natural food, still select similar macronutrient profiles and make ample use of supplemental foods (Figures 1 and 3). This was also reported by Coogan et al. (2018) who observed that the natural diet of wild bears was more varied than the diet of populations consuming anthropogenic foods. Whether this should be perceived as beneficial or not remains to be explored.

4.4 | Implications for the Dietary Macronutrient Profile of Bears Under Human Care

Knowledge of the dietary macronutrient profiles of free-ranging brown bears is indispensable to increase our understanding of their behavior, ecology and biology (e.g., physiological processes related to hibernation). Furthermore, these findings can provide the fundamentals for the development of international dietary guidelines for bears in captivity. A better understanding of the seasonal fluctuation of macronutrients depending on the climatic region where wild European brown bears live, raises the interesting question of which macronutrient profile should be given priority. Do institutions that keep brown bears and provide them with a seasonal diet need to focus on a macronutrient profile corresponding to the climate classification where the facility is located or where the bear originates from, do they follow the macronutrient ratio of brown bear populations consuming supplemented anthropogenic foods or do they provide the same macronutrient ratio all year round with only adjusting the absolute amounts fed according to the period (hyperphagia)? Future research on the effect of dietary regimes on captive bear welfare are warranted to answer these questions.

5 | Conclusion

European brown bears that inhabit different climate regions have different macronutrient profiles in their diets. Hence the presence of a general species-specific nutrient goal or profile regardless of the individual's environmental surroundings cannot be corroborated. Seasonal fluctuations, however, seem to follow similar patterns in every climate region. European bears all seem to forage for a low dietary protein ratio in autumn before hibernation, and bears inhabiting warm regions even attain to this low ratio all year round. Anthropogenic feeds alter macronutrient profiles in a substantial way. Whether this should be considered disadvantageous or not should be further investigated. Furthermore, our findings can provide a basis for dietary guidelines for bears under human care.

Acknowledgements

The authors have nothing to report.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Arnfield, A. 2017. "Köppen Climate Classification." In *Encyclopedia Britannica*, 11th ed.

Ballard, W. B., T. H. Spraker, and K. P. Taylor. 1981. "Causes of Neonatal Moose Calf Mortality in South Central Alaska." *Journal of Wildlife Management* 45: 335–342.

Barboza, P. S., S. D. Farley, and C. T. Robbins. 1997. "Whole-Body Urea Cycling and Protein Turnover During Hyperphagia and Dormancy in Growing Bears (*Ursus americanus* and *U. arctos*)." *Canadian Journal of Zoology* 75: 2129–2136.

Barros, L., A. M. Carvalho, J. S. Morais, and I. C. F. R. Ferreira. 2010. "Strawberry-Tree, Blackthorn and Rose Fruits: Detailed Characterisation in Nutrients and Phytochemicals With Antioxidant Properties." *Food Chemistry* 120: 247–254.

Beck, H. E., N. E. Zimmermann, T. R. McVicar, N. Vergopolan, A. Berg, and E. F. Wood. 2018. "Present and Future Köppen-Geiger Climate Classification Maps at 1-km Resolution." *Scientific Data* 5: 180214.

Blanco, J. C., F. Ballesteros, A. García-Serrano, J. Herrero, C. Nores, and G. Palomero. 2011. "Behaviour of Brown Bears Killing Wild Ungulates in the Cantabrian Mountains, Southwestern Europe." *European Journal of Wildlife Research* 57: 669–673.

Bogdanović, N., A. Zedrosser, A. G. Hertel, and D. Ćirović. 2024. "Cozy Den or Winter Walk: The Effects of Climate and Supplementary Feeding on Brown Bear Winter Behavior." *Journal of Zoology* 323: 292–304.

Bojarska, K., and N. Selva. 2012. "Spatial Patterns in Brown Bear *Ursus arctos* Diet: The Role of Geographical and Environmental Factors." *Mammal Review* 42: 120–143.

Bojarska, K., and N. Selva. 2013. "Correction Factors for Important Brown Bear Foods in Europe." *Ursus (International Association for Bear Research and Management)* 24: 13–15.

Bonan, G. B., and H. H. Shugart. 1989. "Environmental Factors and Ecological Processes in Boreal Forests." *Annual Review of Ecology and Systematics* 20: 1–28.

Bosch, G., E. A. Hagen-Plantinga, and W. H. Hendriks. 2015. "Dietary Nutrient Profiles of Wild Wolves: Insights for Optimal Dog Nutrition?" *British Journal of Nutrition* 113: S40–S54.

Chapron, G., P. Kaczensky, J. D. C. Linnell, et al. 2014. "Recovery of Large Carnivores in Europe's Modern Human-Dominated Landscapes." *Science* 346: 1517–1519.

Cicnjak, L., D. Huber, H. U. Roth, R. L. Ruff, and Z. Vinovrski. 1987. "Food Habits of Brown Bears in Plitvice Lakes National Park, Yugoslavia." Paper presented at International Conference of Bear Research and Management, 7, 221–226.

Ciucci, P., E. Tosoni, G. Di Domenico, F. Quattrociocchi, and L. Boitani. 2014. "Seasonal and Annual Variation in the Food Habits of Apennine Brown Bears, Central Italy." *Journal of Mammalogy* 95: 572–586.

Clauss, M., H. Kleffner, and E. Kienzle. 2010. "Carnivorous Mammals: Nutrient Digestibility and Energy Evaluation." *Zoo Biology* 29: 687–704.

Clevenger, A. P., F. J. Purroy, and M. R. Pelton. 1992. "Food Habits of Brown Bears (*Ursus arctos*) in the Cantabrian Mountains, Spain." *Journal of Mammalogy* 73: 415–421.

Coogan, S. C. P., D. Raubenheimer, G. B. Stenhouse, N. C. Coops, and S. E. Nielsen. 2018. "Functional Macronutritional Generalism in a Large Omnivore, the Brown Bear." *Ecology and Evolution* 8: 2365–2376.

Coogan, S. C. P., D. Raubenheimer, G. B. Stenhouse, and S. E. Nielsen. 2014. "Macronutrient Optimization and Seasonal Diet Mixing in a Large Omnivore, the Grizzly Bear: A Geometric Analysis." *PLoS One* 9: e97968.

Cotter, S. C., S. J. Simpson, D. Raubenheimer, and K. Wilson. 2011. "Macronutrient Balance Mediates Trade-Offs Between Immune Function and Life History Traits." *Functional Ecology* 25: 186–198.

Dahle, B., O. J. Sørensen, E. H. Wedul, J. E. Swenson, and F. Sandegren. 1998. "The Diet of Brown Bears *Ursus arctos* in Central Scandinavia: Effect of Access to Free-Ranging Domestic Sheep *Ovis aries*." *Wildlife Biology* 4: 147–158.

DeAngelis, D. 2019. *The Boreal Forest Ecosystem. Encyclopedia of Ecology*, 479–483. Elsevier.

Delgado, M. M., G. Tikhonov, E. Meyke, et al. 2018. "The Seasonal Sensitivity of Brown Bear Denning Phenology in Response to Climatic Variability." *Frontiers in Zoology* 15: 41.

Denny, C. K., G. B. Stenhouse, and S. E. Nielsen. 2018. "Scales of Selection and Perception: Landscape Heterogeneity of an Important Food Resource Influences Habitat Use by a Large Omnivore." *Wildlife Biology* 2018: 1–10.

Depauw, S., M. Hesta, K. Whitehouse-Tedd, L. Vanhaecke, A. Verbrugghe, and G. P. J. Janssens. 2013. "Animal Fibre: The Forgotten Nutrient in Strict Carnivores? First Insights in the Cheetah." *Journal of Animal Physiology and Animal Nutrition* 97: 146–154.

De Cuyper, A., D. Strubbe, M. Clauss, et al. 2023. "Nutrient Intake and Its Possible Drivers in Free-Ranging European Brown Bears (*Ursus arctos* Arctos)." *Ecology and Evolution* 13: e10156.

de-Oliveira, L. D., F. S. Takakura, E. Kienzle, et al. 2012. "Fibre Analysis and Fibre Digestibility in Pet Foods—A Comparison of Total Dietary Fibre, Neutral and Acid Detergent Fibre and Crude Fibre." *Journal of Animal Physiology and Animal Nutrition* 96: 895–906.

Elfström, M., J. E. Swenson, and J. P. Ball. 2008. "Selection of Denning Habitats by Scandinavian Brown Bears *Ursus arctos*." *Wildlife Biology* 14: 176–187.

Elgmork, K., and J. Kaasa. 1992. "Food Habits and Foraging of the Brown Bear *Ursus arctos* in Central South Norway." *Ecography* 15: 101–110.

Erlenbach, J. A., K. D. Rode, D. Raubenheimer, and C. T. Robbins. 2014. "Macronutrient Optimization and Energy Maximization Determine Diets of Brown Bears." *Journal of Mammalogy* 95: 160–168.

Fowler, M. 2011. *Medicine and Surgery of Camelids*, 3rd ed. Wiley-Blackwell.

Friebe, A., J. E. S. Swenson, and F. Sandegren. 2001. "Denning Chronology of Female Brown Bears in Central Sweden." *Ursus (International Association for Bear Research and Management)* 12: 37–45.

Hewitt, D. G., and C. T. Robbins. 1996. "Estimating Grizzly Bear Food Habits From Fecal Analysis." *Wildlife Society Bulletin* 24: 547–550.

Hilderbrand, G. V., D. D. Gustine, B. Mangipane, et al. 2018. "Plasticity in Physiological Condition of Female Brown Bears Across Diverse Ecosystems." *Polar Biology* 41: 773–780.

Hilderbrand, G. V., K. Joly, M. S. Sorum, M. D. Cameron, and D. D. Gustine. 2019. “Brown Bear (*Ursus arctos*) Body Size, Condition, and Productivity in the Arctic, 1977–2016.” *Polar Biology* 42: 1125–1130.

Hissa, R. 1997. “Physiology of the European Brown Bear (Ursus arctos arctos).” *Annales Zoologici Fennici* 34: 267–287.

Huber, D., and H. U. Roth. 1997. “Denning of Brown Bears in Croatia.” *Bears: Their Biology and Management* 9: 79–83.

Jensen, K., D. Mayntz, S. Toft, et al. 2012. “Optimal Foraging for Specific Nutrients in Predatory Beetles.” *Proceedings of the Royal Society B: Biological Sciences* 279: 2212–2218.

Kavčič, I., M. Adamič, P. Kaczensky, M. Krofel, M. Kobal, and K. Jerina. 2015. “Fast Food Bears: Brown Bear Diet in a Human-Dominated Landscape With Intensive Supplemental Feeding.” *Wildlife Biology* 21: 1–8.

Kottek, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel. 2006. “World Map of the Köppen-Geiger Climate Classification Updated.” *Meteorologische Zeitschrift* 15: 259–263.

Kuhnlein, H. 2002. “Macronutrient, Mineral and Fatty Acid Composition of Canadian Arctic Traditional Food.” *Journal of Food Composition and Analysis* 15: 545–566.

Linnell, J. D. C., R. Aanes, and R. Andersen. 1995. “Who Killed Bambi? The Role of Predation in the Neonatal Mortality of Temperate Ungulates.” *Wildlife Biology* 1: 209–223.

López-Alfaro, C., S. C. P. Coogan, C. T. Robbins, J. K. Fortin, and S. E. Nielsen. 2015. “Assessing Nutritional Parameters of Brown Bear Diets Among Ecosystems Gives Insight Into Differences Among Populations.” *PLoS One* 10: e0128088.

López-Alfaro, C., C. T. Robbins, A. Zedrosser, and S. E. Nielsen. 2013. “Energetics of Hibernation and Reproductive Trade-Offs in Brown Bears.” *Ecological Modelling* 270: 1–10.

Mateo Sánchez, M. C., S. A. Cushman, and S. Saura. 2014. “Scale Dependence in Habitat Selection: The Case of the Endangered Brown Bear (*Ursus arctos*) in the Cantabrian Range (NW Spain).” *International Journal of Geographical Information Science* 28: 1531–1546.

McDonald, P., J. F. D. Greenhalgh, C. A. Morgan, R. Edwards, L. Sinclair, and R. Wilkinson. 2011. *Animal Nutrition*, 7th ed. Pearson Education.

Mealey, S. P. 1980. “The Natural Food Habits of Grizzly Bears in Yellowstone National Park, 1973-74.” *Bears: Their Biology and Management* 4: 281.

Mikkelsen, A. J., K. A. Hobson, A. Sergiel, A. G. Hertel, N. Selva, and A. Zedrosser. 2024. “Testing Foraging Optimization Models in Brown Bears: Time for a Paradigm Shift in Nutritional Ecology?” *Ecology* 105: e4228.

Naves, J., A. Fernández-Gil, C. Rodríguez, and M. Delibes. 2006. “Brown Bear Food Habits at the Border of Its Range: A Long-Term Study.” *Journal of Mammalogy* 87: 899–908.

Niedziałkowska, M., M. W. Hayward, T. Borowik, W. Jędrzejewski, and B. Jędrzejewska. 2019. “A Meta-Analysis of Ungulate Predation and Prey Selection by the Brown Bear *Ursus arctos* in Eurasia.” *Mammal Research* 64: 1–9.

Nores, C., F. Ballesteros, J. C. Blanco, A. García-Serrano, J. Herrero, and G. Palomero. 2010. “Evidence of Non-Hibernation in Cantabrian Brown Bears.” *Acta Theriologica* 55: 203–209.

NRC. 2012. *Nutrient Requirements of Swine*. National Academy Press.

Papakosta, M., K. Kitikidou, D. Bakaloudis, and C. Vlachos. 2014. “Dietary Variation of the Stone Marten (*Martes foina*): A Meta-Analysis Approach.” *Wildlife Biology in Practice* 10: 85–101.

Paralikidis, N. P., N. K. Papageorgiou, V. J. Kontsiotis, and A. C. Tsiompanoudis. 2010. “The Dietary Habits of the Brown Bear (*Ursus arctos*) in Western Greece.” *Mammalian Biology* 75: 29–35.

Peel, M. C., B. L. Finlayson, and T. A. Mcmahon. 2007. “Updated World Map of the Köppen-Geiger Climate Classification.” *Hydrology and Earth System Sciences* 11: 1633–1644.

Persson, I. L., S. Wikan, J. E. Swenson, and I. Mysterud. 2001. “The Diet of the Brown Bear *Ursus arctos* in the Pasvik Valley, Northeastern Norway.” *Wildlife Biology* 7: 27–37.

Plantinga, E. A., G. Bosch, and W. H. Hendriks. 2011. “Estimation of the Dietary Nutrient Profile of Free-Roaming Feral Cats: Possible Implications for Nutrition of Domestic Cats.” *British Journal of Nutrition* 106: S35–S48.

Prosky, L., N. G. Asp, I. Furda, J. W. Devries, T. F. Schweizer, and B. F. Harland. 1985. “Determination of Total Dietary Fiber in Foods and Food-Products—Collaborative Study.” *Journal of AOAC International* 68: 677–679.

Raubenheimer, D., S. J. Simpson, and D. Mayntz. 2009. “Nutrition, Ecology and Nutritional Ecology: Toward an Integrated Framework.” *Functional Ecology* 23: 4–16.

Remonti, L., A. Balestrieri, D. Raubenheimer, and N. Saino. 2016. “Functional Implications of Omnivory for Dietary Nutrient Balance.” *Oikos* 125: 1233–1240.

Robbins, C. T., A. L. Christian, T. G. Vineyard, et al. 2022. “Ursids Evolved Early and Continuously to Be Low-Protein Macronutrient Omnivores.” *Scientific Reports* 12: 15251.

Robbins, C. T., J. K. Fortin, K. D. Rode, S. D. Farley, L. A. Shipley, and L. A. Felicetti. 2007. “Optimizing Protein Intake as a Foraging Strategy to Maximize Mass Gain in an Omnivore.” *Oikos* 116: 1675–1682.

Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. “Behavioral Responses of Brown Bears Mediate Nutritional Effects of Experimentally Introduced Tourism.” *Biological Conservation* 133: 70–80.

Rode, K. D., C. T. Robbins, C. A. Stricker, B. D. Taras, and T. N. Tollefson. 2021. “Energetic and Health Effects of Protein Overconsumption Constrain Dietary Adaptation in an Apex Predator.” *Scientific Reports* 11: 15309.

Rothman, J. M., A. J. Plumptre, E. S. Dierenfeld, and A. N. Pell. 2007. “Nutritional Composition of the Diet of the Gorilla (*Gorilla beringei*): A Comparison Between Two Montane Habitats.” *Journal of Tropical Ecology* 23: 673–682.

Schwarm, A., S. Ortmann, W. Rietschel, R. Kühne, G. Wibbelt, and M. Clauss. 2010. “Function, Size and Form of the Gastrointestinal Tract of the Collared *Pecari tajacu* (Linnaeus 1758) and White-Lipped Peccary *Tayassu pecari* (Link 1795).” *European Journal of Wildlife Research* 56: 569–576.

Selva, N., T. Berezowska-Cnota, and I. Elguero-Claramunt. 2014. “Unforeseen Effects of Supplementary Feeding: Ungulate Baiting Sites as Hotspots for Ground-Nest Predation.” *PLoS One* 9: e90740.

Senior, A. M., C. E. Grueber, G. Machovsky-Capuska, S. J. Simpson, and D. Raubenheimer. 2016. “Macronutritional Consequences of Food Generalism in an Invasive Mammal, the Wild Boar.” *Mammalian Biology* 81: 523–526.

Simpson, S. J., R. M. Sibly, K. P. Lee, S. T. Behmer, and D. Raubenheimer. 2004. “Optimal Foraging When Regulating Intake of Multiple Nutrients.” *Animal Behaviour* 68: 1299–1311.

Skuban, M., S. Finďo, and M. Kajba. 2016. “Human Impacts on Bear Feeding Habits and Habitat Selection in the Poľana Mountains, Slovakia.” *European Journal of Wildlife Research* 62: 353–364.

Stenset, N. E., P. N. Lutnæs, V. Bjarnadóttir, et al. 2016. “Seasonal and Annual Variation in the Diet of Brown Bears *Ursus arctos* in the Boreal Forest of Southcentral Sweden.” *Wildlife Biology* 22: 107–116.

Štofik, J., J. Merganič, K. Merganičová, and M. Saniga. 2013. "Seasonal Changes in Food Composition of the Brown Bear (*Ursus arctos*) From the Edge of Its Occurrence—Eastern Carpathians (Slovakia)." *Folia Zoologica* 62: 222–231.

Swenson, J., B. Dahle, H. Busk, et al. 2007. "Predation on Moose Calves by European Brown Bears." *Journal of Wildlife Management* 71: 1993–1997.

Swenson, J. E., M. Adamič, D. Huber, and S. Stokke. 2007. "Brown Bear Body Mass and Growth in Northern and Southern Europe." *Oecologia* 153: 37–47.

Swenson, J. E., A. Jansson, R. Riig, and F. Sandegren. 1999. "Bears and Ants: Myrmecophagy by Brown Bears in Central Scandinavia." *Canadian Journal of Zoology* 77: 551–561.

Tremblay, Y., and Y. Cherel. 2003. "Geographic Variation in the Foraging Behaviour, Diet and Chick Growth of Rockhopper Penguins." *Marine Ecology Progress Series* 251: 279–297.

Trites, A. W., and R. Joy. 2005. "Dietary Analysis From Fecal Samples: How Many Scats Are Enough?" *Journal of Mammalogy* 86: 704–712.

Van Soest, P. J., and R. W. McQueen. 1973. "The Chemistry and Estimation of Fibre." *Proceedings of the Nutrition Society* 32: 123–130.

Vulla, E., K. A. Hobson, M. Korsten, et al. 2009. "Carnivory Is Positively Correlated With Latitude Among Omnivorous Mammals: Evidence From Brown Bears, Badgers and Pine Martens." *Annales Zoologici Fennici* 46: 395–415.

Zalewski, A. 2005. "Geographical and Seasonal Variation in Food Habits and Prey Size of European Pine Martens." In *Martens and Fishers (Martes) in Human-Altered Environments*, 77–98. Springer.

Zedrosser, A., B. Dahle, J. E. Swenson, and N. Gerstl. 2001. "Status and Management of the Brown Bear in Europe." *Ursus (International Association for Bear Research and Management)* 12: 9–20.

Zhou, Y. B., C. Newman, W. T. Xu, et al. 2011. "Biogeographical Variation in the Diet of Holarctic martens (Genus Martes, Mammalia: Carnivora: Mustelidae): Adaptive Foraging in Generalists: Biogeographical Variation in the Diet of Holarctic martens." *Journal of Biogeography* 38: 137–147.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.