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Short Communication

How absolute biomass intake can alter nutrient profile interpretation in free-ranging species: the case of protein intake in brown bears

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If an animal eats a large amount of a diet of a low content of a macronutrient, it can still ingest a considerable amount of that macronutrient. Various animals have been shown to balance nutrient content with intake in this way. We use the brown bear *Ursus arctos* as a model species, given their recent classification as 'low protein omnivores', to show how taking biomass intake into account can affect macronutrient intake interpretation. We 1) calculated absolute protein intake from published results of self-selection diet studies with bears in captivity and 2) modelled absolute protein intake of Swedish brown bears in autumn while binging on a berry diet of low protein concentrations. In feeding experiments in captivity, the self-selected macronutrient composition of brown bear diets are characterized by protein percentages (both on a dry matter and metabolizable energy basis) that appear low when compared to diets of carnivores. However, when taking into account absolute food intake and expressing this as daily protein intake per metabolic body mass (33–117 g/kg$^{0.75}$/day), protein intake was considerably higher than established minimum requirements for domestic dogs and cats (2.6–3.8 g/kg$^{0.75}$/day) – carnivores one would not consider 'low protein specialists'. Our hypothetical berry model yielded a protein intake of 3.2–9.7 g/kg$^{0.75}$/day, which is lower than the outcomes from the self-selection trials but still comparable to established requirements of domestic dogs and cats. Instead of perceiving bears as low-protein consumers, it might be more accurate to perceive them as temporary hyperphagia specialists for which low protein concentrations are necessary to avoid dramatically overshooting protein requirements. Including absolute food intake in diet determination offers important nuances in result interpretation. When coining labels to categorize animals, it may be advisable to not only consider nutrient concentrations but also absolute intake.

Keywords: biomass intake, macronutrient, protein, *Ursus arctos*

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Introduction

Dietary nutrient 'balance' is an essential part of the fitness of species, including their pattern of reproduction, survival and longevity (Cook et al. 2004, Lee et al. 2008, Piper et al. 2011, Jensen et al. 2012, Solon-Biet et al. 2014, Fontana and Partridge 2015, Moatt et al. 2019). An increasing amount of research has therefore gone beyond the study of mere dietary food items and looked into the dietary macronutrient profiles of free-ranging species (Rothman et al. 2008, Bosch et al. 2015, Coogan et al. 2018, Gazzola-Balestrieri et al. 2020, Robbins et al. 2022a). Typically, dietary macronutrient profiles are expressed as % dry matter basis (DM) or % of metabolizable energy (ME), which is necessary to compare diets within or between species on the same basis, and to estimate how much of a diet an animal must eat to meet its requirements.

However, one needs to be cautious with the use and interpretation of solely a percentual composition, which does not necessarily indicate absolute nutrient intake, nor does it equal nutrient requirements. As once stated by Clauss et al. (2010), animals do not eat percentages but amounts. For instance, in a study with mountain gorillas *Gorilla beringei*, it was shown that even though protein concentration did not differ in the diet of different subgroups, some achieved a distinctively higher protein intake by ingesting more of their diet (Rothman et al. 2008). Spider monkeys *Ateles chamek* kept their protein intake constant by adjusting their biomass intake to the protein content of different food items (Felton et al. 2009). These examples highlight the importance of considering biomass intake or the 'amount eaten', which is also a well-known principle in domestic nutrition research where nutrient requirements are given as amounts (NRC 2006, 2007, 2012). Nevertheless, because the ingredient and hence nutrient composition of a diet is typically easier to reconstruct in natural settings than it is to quantify intake, the use of biomass intake in macronutrient profile interpretations of free-ranging species may still be rare.

A number of recent publications suggests that brown bears *Ursus arctos*, and ursids in general, have evolved into 'low protein macronutrient omnivores' (Robbins et al. 2007, 2022a, Erlenbach et al. 2014, Rode et al. 2021, Mikkelsen et al. 2024). This particular line of bear nutrition research took off with observations of free-ranging grizzly bears consuming spawning salmon interspersed with berries in the autumn season (Rode et al. 2006, Fortin et al. 2007). This in itself was remarkable, because if one considers the optimal foraging theory and assumes that animals forage for the highest energy return (Pyke et al. 1977), a salmon-only diet would be 'more optimal'. Several studies with captive bears followed and showed that when given a choice between diet items that were offered for ad libitum consumption, bears maximize energy intake while selecting diets of an average protein content at 19 or 22% in DM and 17 or 21% of ME (Robbins et al. 2007, Erlenbach et al. 2014). When comparing these values against the self-selected diets of other carnivores such as domestic dogs (protein 30% of ME), domestic cats (52% of ME) or mink (35% of ME), the bear diets appear relatively low in protein (Erlenbach et al. 2014). This was observed during experiments in autumn (Robbins et al. 2007, Erlenbach et al. 2014) but also in one experiment conducted in spring (Erlenbach et al. 2014). More so, consumption of such low protein diets was linked to efficient accretion of mass, which is particularly beneficial in the pre-hibernation phase of bears (Felicetti et al. 2003, Erlenbach et al. 2014).

Today, many free-ranging populations have been studied for their dietary macronutrient profiles, which reveal that although low dietary protein levels are definitely present, this greatly depends on the season (mainly in autumn during hyperphagia) and the population under study (Coogan et al. 2018, De Cuyper et al. 2023, Verbist et al. unpubl.). Such variation cautions against generalizing a 'low-protein omnivore' label at all times and locations for brown bears. The interpretation of bears as low protein consumers hinges specifically on the comparison with self-selected diets of domestic dogs, cats or mink (35% of ME) (Erlenbach et al. 2014), and on the suggestion that high protein diets might contribute to health problems documented in zoo-managed bears (Rode et al. 2021, Robbins et al. 2022a, 2022b). By contrast, the fact that all these self-selected diets have distinctively higher protein levels than the documented minimum protein requirements for domestic dogs (8–10% DM, 8–10% ME, Table 15-5 in NRC 2006) has received little attention.

We hypothesized that, within brown bears as a model species, when considering the biomass intake of low protein diets (% on DM basis) from self-selection studies in captivity and free-ranging situations, protein intake will still be considerable and meet the protein requirements that were established for other carnivore species that are considered 'high protein consumers' like dogs and cats (NRC 2006). We therefore pursued a double strategy. First, we calculated the absolute daily protein intake per metabolic body mass in bears of the studies in captivity of Robbins et al. (2007) and Erlenbach et al. (2014), and compared it with the protein intake of other carnivore species (including maintenance requirements of domestic dogs and cats, Table 15-5 and Table 15-12, respectively, in NRC 2006). Second, we performed a simple calculation exercise that focused on the autumn berry-binge event in Swedish brown bears (Hertel et al. 2016, Stenset et al. 2016, De Cuyper et al. 2023). The macronutrient profile of bears during berry-binging has already been calculated and can be classified as a distinctively low protein diet (12.2% on DM basis; De Cuyper et al. 2023), being even lower in protein content than those reported in self-selecting experiments.

Methods

Protein intake from self-selection studies

The self-selection studies with brown bears reported in Robbins et al. (2007) and Erlenbach et al. (2014) were used to calculate the daily protein intake (g/metabolic body mass ($kg^{0.75}$)) for several experimental diets. For every study and experimental diet, the average body mass of bear individuals was extracted as well as the average total fresh matter intake (i.e. absolute biomass intake; as % body mass) which allowed to estimate absolute food intake as:

Absolute food intake (kg/day) = total fresh matter intake/day (% body mass) × body mass (kg)

Subsequently, the average % DM of food items and the % crude protein (CP) (on a DM basis) of the ingested diet were extracted and used to calculate the average daily DM and protein intake as:

DM intake (kg/day) = absolute food intake (kg/day) × % DM
CP intake (kg/day) = DM intake (kg/day) × % CP
CP intake (g/kg$^{0.75}$/day) = (CP intake (kg/day) × 1000)/(body mass)$^{0.75}$

The protein intake of captive brown bears was put into comparison with several protein intake data of domestic dogs and wolves *Canis lupus*, of domestic and feral cats, and two other ursid species (i.e. the sloth bear *Melursus ursinus* and the giant panda *Ailuropoda melanoleuca*) using the experimental data from Robbins et al. (2022a). These calculations were done in a similar way except that the daily energy intake (kJ/kg$^{0.75}$/day) and energy density of diets (kJ/100 gDM) were used to estimate DM intake (g/day) for studies with domestic dogs, wolves, and domestic and feral cats. From there on, calculations are similar as mentioned above (Table 1). The minimum requirements and recommended allowances for protein intake of domestic dogs and cats are extracted from the Table 15-5 and Table 15-12, respectively, of the NRC (2006), and provide a basis for comparison as these species are typically not considered low protein consumers.

Hypothetical protein intake during berry-binging as a model for low protein diets

The macronutrient composition of berries (*Vaccinium* sp.) was taken from De Cuyper et al. (2023). Berries of the genus *Vaccinium* sp. have an average of 15.3% DM and a macronutrient composition (% on DM basis) of 5.2% CP, 2.5% crude fat, 67.5% easily digestible carbohydrates, 23.2% total dietary fiber, and 1.6% ash. The apparent DM and CP digestibility can be estimated as 63.8% and 18.9%, respectively, following digestion experiments by Pritchard and Robbins (1990).

For the modelling exercise, we assumed a hypothetical 100% berry diet, based on Hertel et al. (2016), Stenset et al. (2016), De Cuyper et al. (2023). The absolute biomass intake of berries by Swedish brown bears during autumn was calculated via two methods chosen to represent 1) a realistic and 2) a hypothetical maximum intake level. We chose not to work with biomass estimations from dietary remains in the feces, given the errors and limitations that are associated with the latter (Klare et al. 2011). Methods were:

1) Berry intake by captive brown bears foraging on berry bushes can be estimated as 30 g of berries per minute (with a single berry weighing 0.5 g) (Welch et al. 1997). Foraging time for berries was estimated as 14 h per day (Stelmock and Dean 1986). Berry intake, DM intake, CP intake, digestible DM (dDM) intake and digestible CP (dCP) intake were calculated as:
   Berry intake (kg/day) = 30 g × 60 minutes × 14 hours
   DM intake (kg/day) = Berry intake (kg/day) × 15.3 (% DM)
   CP intake (kg/day) = DM intake (kg/day) × 5.2 (% CP)
   CP intake (g/kg$^{0.75}$/day) = (CP intake (kg/day) × 1000) / body mass$^{0.75}$
   dDM intake (kg/day) = DM intake (kg/day) × 63.8 (% digestibility)
   dCP intake (kg/day) = CP intake (kg/day) × 18.9 (% digestibility)
2) Using of the formula of maximum daily food intake (kg/bear/day) = 0.66 × body mass (kg)$^{0.86}$ if berries are offered for ad libitum consumption in the enclosure (Welch et al. 1997).

For these approaches, we use a fictional Scandinavian male brown bear of 250 kg (Swenson et al. 2007).

Results

The protein intake of brown bears during self-selection experiments ranged from 33 to 117 g/kg$^{0.75}$/day and thus exceeded the minimum requirement of domestic dogs and cats (2.62 and 3.97 g/kg$^{0.75}$/day, respectively) by more than tenfold, and all other protein intake values calculated for domestic dogs and domestic and feral cats (5.2 to 15.9 g/kg$^{0.75}$/day) (Table 1). In this respect, the bear data was similar to the protein intake of free-ranging wolves. The latter was estimated at 37 g/kg$^{0.75}$/day (i.e. about tenfold the minimum domestic dog requirement), albeit at dramatically higher dietary protein levels than those of the experimental bears, emphasizing the effect of the bears' comparatively high food intake. The protein intake of the sloth bear and giant panda (9.3 and 11.3 g/kg$^{0.75}$/day, respectively) was lower than the ranges found for brown bears in the self-selection experiments (33 to 117 g/kg$^{0.75}$/day) but again distinctively higher than the nominal maintenance requirements for domestic dogs and cats.

Our fictional CP intake calculations in the berry-binge autumn period calculated with method 1 (3.18 g/kg$^{0.75}$/day, Table 2) is among the lowest of all calculated results (Table 1) but still higher than the minimal protein requirements of domestic dogs (2.62 g CP/kg$^{0.75}$/day; Table 1). Method 2 renders a higher protein intake (9.70 g/kg$^{0.75}$/day, Table 2) which is comparable to other carnivore species (Table 1) and higher than the minimal protein requirements of domestic dogs and cats (Table 1). If one considers, however, the low protein digestibility of berries in our theoretical model (18.9%), then the digestible protein intake would be below the minimum requirements of domestic carnivores (0.60 to 1.91 g digestible protein/kg$^{0.75}$/day).

Table 1. Dietary protein concentrations and protein intake for bears, domestic dogs, domestic and feral cats and wolves based on literature data and this study.

Species	Condition	Dietary protein (% DM basis)	Dietary protein (% ME basis)*	Daily protein intake (g/metabolic body mass ($kg^{0.75}$))	Source
Brown bear	Self-selection diet study - salmon, apples and beef fat (ad libitum, autumn) [a]	16	11	33.23	Erlenbach et al. 2014
	Self-selection diet study - salmon, apples and beef fat (ad libitum, spring) [b]	22	18	45.69	
	Self-selection diet study - beef, bread and pork fat (ad libitum, autumn) [c]	24	15	33.56	
	Self-selection diet study - salmon and salmon-oil (ad libitum, autumn) [d]	31	20	117.18	
Brown bear	Self-selection diet study - salmon and apples (ad libitum, autumn) [e]	19	21	43.27	Robbins et al. 2007
Brown bear	Theoretical berry model	5.2	6.6	3.18–9.70	this study
Domestic dog	Minimal requirement	8	8	2.62	NRC 2006
	Recommended allowance	10	10	3.28	
Domestic dog	Evaluation commercial dog foods [f]	28.2	30.7	8.4	Kazimierska et al. 2021
Wolf	Diet of wild wolves [g]	67.2	53.9	37.14	Bosch et al. 2015
Domestic cat	Minimal requirement [h]	16	16	3.97	NRC 2006
	Recommended allowance	20	20	4.96	
Domestic cat	Feeding experiment with mice diet [i]	56.5	49.3	5.2	D'Hooghe et al. 2024
Feral cat	Diet of feral cats [j]	60	64.3	15.9	D'Hooghe 2024
Sloth bear	Self-selection diet study - apples, avocados, yams and whey solution (ad libitum) [k]	14	12	9.32	Robbins et al. 2022a
Giant panda	Diet study - bamboo (ad libitum) [l]	7.63	20	11.30	Robbins et al. 2022a, Christian 2017

[a] Based on a 233 kg bear (average of bear mass in experiment); fresh matter intake of 12% of body mass; an average % DM of diet items of 44.3% (no proportional fresh matter intake of individual diet items available)

[b] Based on a 233 kg bear (average of bear mass in experiment); fresh matter intake of 12 % of body mass; an average % DM of diet items of 44.3% (no proportional fresh matter intake of individual diet items available)

[c] Based on a 233 kg bear (average of bear mass in experiment); fresh matter intake of 6% of body mass; an average % DM of diet items of 59.66% (no proportional fresh matter intake of individual diet items available)

[d] Based on a 233 kg bear (average of bear mass in experiment); fresh matter intake of 15% of body mass; an average % DM of diet items of 64.5% (no proportional fresh matter intake of individual diet items available)

[e] Based on a 245 kg bear (average of bear mass in experiment); fresh matter intake of 30% of body mass; 84% and 16% proportional fresh matter intake of apples and salmon, respectively; 17.4% DM in apples and 28.5% DM in salmon

[f] Based on an average of 28.2 g CP/100 gDM; 369.44 kcal/100 g DM; energy intake of 110 kcal/$kg^{0.75}$

[g] Based on an average of 67 .2 g CP/100 gDM; 2085 kJ/100g DM; energy intake of 19.442 kJ/day (field metabolic rate from Nagy et al. (1999) used in De Cuyper et al. (2019) and a 43.28 kg wolf De Cuyper et al. (2019).

[h] Based on a metabolic mass of $kg^{0.67}$

[i] Based on a 4.4 kg cat; an average of 56.5g CP/100 g DM; intake of 28 g DM/day

[j] Based on an average of 60 g CP/100 g DM; 1560 kJ/100 g DM; energy intake of 1258 kJ/day (Plantinga et al. 2011) and a 4.4 kg cat

[k] Based on a 115.8 kg bear (average of bear mass in experiment); an average DM intake of 1849.6 g/day

[l] Based on a 97.9 kg bear (average of bear mass in experiment); an average DM intake of 4610.0 g/day and average CP on DM basis of 7.63% taken from Christian et al. (2017); protein on ME basis taken from Robbins et al. (2022)

*Whenever the protein value on ME basis was not given by the literature source, we used the unmodified Atwater factors (16.72 kJ/g protein) for ME base calculations.

Discussion

We show that including biomass intake when studying the macronutrient concentration of animal diets can substantially influence the interpretation of a species' dietary adaptation. We use brown bears as a model species since a substantial amount of research has been used to claim that bears are 'low protein macronutrient omnivores' (Robbins et al. 2007, 2022a, Erlenbach et al. 2014). However, the effect of biomass intake on such low protein diets has not been discussed. Studies in free-ranging primates, for instance, showed the importance of measuring absolute food intake

Table 2. Absolute fresh matter, dry matter (DM), crude protein (CP) and digestible dry matter and crude protein (dDM, dCP) intake of berries (*Vaccinium* sp.) by a hypothetical Scandinavian male brown bear *Ursus arctos* of 250 kg during the autumn berry-binging period calculated with two berry intake rate methods (Welch et al. 1997).

Intake (kg/day)	Method 1	Method 2
Absolute fresh matter intake	25.2	76.2
Absolute DM intake	3.86	11.66
Absolute CP intake	0.20	0.61
Absolute dDM intake	2.46	7.44
Absolute dCP intake	0.038	0.12
Intake ($g/kg^{0.75}/day$)		
Absolute CP intake	3.18	9.70

Method 1 estimates absolute biomass intake as 30 g of berries per minute and a foraging time of 14 h per day; method 2 estimates absolute biomass intake (kg/bear/day) as $= 0.66 \times$ body mass $(kg)^{0.86}$ and uses a fictional Scandinavian male bear mass of 250 kg. Digestibility coefficients of dry matter and protein are 63.8% and 18.9%, respectively (Pritchard and Robbins 1990).

(Rothman et al. 2008, Felton et al. 2009). Bears are particularly interesting in this respect, given their seasonal hyperphagia which is a period of high biomass intake (Barboza et al. 1997, González-Bernardo et al. 2020). When bears select a low protein diet in combination with a high biomass intake, in particular during the autumn hyperphagia period, they can still ingest a considerable amount of (digestible) protein. Actually, in self-selection experiments whose results were interpreted as indicators for a propensity for low protein diet in brows bears, the bears ingested protein at amounts far exceeding minimum domestic dog requirements. Only for our theoretical model, which used a pure berry diet of low protein concentration *and* low protein digestibility, did bears come close to, or fall below, domestic dog minimum protein intakes. Hence, generalizing that brown bears are low-protein consumers should be done with caution because absolute biomass intake cannot be neglected. Rather than bears being low protein specialists, they could be perceived as 'high biomass intake' specialists that consume low to moderate protein diets during hyperphagic periods to not overshoot absolute protein requirements excessively, with all its health consequences (Rode et al. 2021, Robbins et al. 2022b).

Estimating biomass intake in free-ranging settings is cumbersome and labor intensive. Direct measurements or observations would be most accurate (Klare et al. 2011) and are feasible under human care conditions. However, they are logistically very difficult in free-ranging specimens. Feces remain the most non-invasive, accessible and informative sample type that can be used to predict diets of free-ranging animals (Reid et al. 2023). There are established formulas or coefficients to calculate the actual biomass or food item intake per fecal sample for wild animals (e.g. the use of allometric formulas to estimate prey biomass intake from fecal analysis for several terrestrial and marine carnivore species, Bowen and Iverson 2013, Chakrabarti et al. 2016). For brown bears specifically, correction factors have been established to calculate the estimated dietary content (EDC) of food items in their diets (Hewitt and Robbins 1996). The latter is typically used for estimating the proportional diet item composition of brown bear diets (Hewitt and Robbins 1996, Bojarska and Selva 2013, Coogan et al. 2018, De Cuyper et al. 2023). Feces of bears are first evaluated in terms of proportional composition of dietary remains, which is then corrected for digestibility via correction factors (Hewitt and Robbins 1996, Bojarska and Selva 2013). This then renders estimates of biomass intake per diet item per volume of feces, which finally allows a percentual composition of items in the diet on a DM basis. From the latter, macronutrient profiles are then calculated. There are various methodologies for studying the "food item composition" of a species' free-ranging diet, ranging from direct methods such as live tracking and observing animals during feeding events (Jordan 2005) or analyzing feces visually (both macroscopically or microscopically) (Phillips and Mcgrew 2014, Stenset et al. 2016), to more 'advanced' methods such as the analysis of stable isotopes (SI) in feces or other tissues (Meckstroth et al. 2007), the analysis of feces or gut content with DNA metabarcoding (Elfström et al. 2014, Forin-Wiart et al. 2018), or scanning feces with near infrared spectroscopy (NIRS). Each method has its own setbacks and strengths to determine diet composition, and at some level, food item composition can be converted into the dietary macronutrient composition. Yet, when it comes to determining more detailed dietary characteristics that are essential in the study of species' nutritional requirements such as biomass intake and digestibility (NRC 1994, 2001, 2006, 2007, 2012, McDonald et al. 2011), these methods fall short. Using them to determine absolute nutrient intake would always necessitate knowing with certainty the total volume of feces defecated in an appropriate period (e.g. a week) in conjunction with digestibility correction factors.

The methodologies used in this study do entail several constraints. The calculations with the published data from Robbins et al. (2007) and Erlenbach et al. (2014) were done with average bear mass (kg) and average absolute food intakes (% body mass). Given the range of individual bear mass and food intakes in these studies, working with averages might lead to calculation biases in protein intake. However, when we calculated protein intake for the minimum and maximum bear mass in combination with both the min. and max. food intake, protein intakes ranged from min. 28.2 to 59.4 $g/kg^{0.75}/day$ in Robbins et al.'s (2007) data in comparison to the 43.2 $g/kg^{0.75}/day$ protein intake based on averages. For the Erlenbach et al. (2014) data for 4 types of diets, the protein intake ranged from 29.8 to 124.3 $g/kg^{0.75}/day$ for calculations based on minimum and maximum values in comparison to 33.2 to 117.2 $g/kg^{0.75}$ based on averages. As such, the use of averages does not influence our conclusions. Our berry biomass estimation exercise was focused on Swedish brown bears which are known to almost exclusively feed on berries in autumn (Stenset et al. 2016, De Cuyper et al. 2023). This calculation is particularly straightforward given the uniformity of this diet, the low protein content of a berry-only diet (De Cuyper et al. 2023) and high intakes typically seen prehibernation. Additionally, the work of Welch et al. (1997) that evaluated intake rates of bears eating fruits (from apples to berries) gave practical tools to calculate absolute berry intake, and with this, absolute (digestible) protein intake. The methodology we used in this calculation exercise includes several estimations and assumptions. Such as, we used berry intake rates from grizzly bears under human care eating slightly bigger berries than the ones found in Sweden (Welch et al. 1997) and we used the macronutrient composition and digestibility of *Vaccinium* sp. (Pritchard and Robbins 1990, De Cuyper et al. 2023) whereas brown bears in Sweden consume a mixture of bilberry *V. myrtillus*, lingonberry *V. vitis-idaea* and crowberry *Empetrum nigrum* (Hertel et al. 2016, Stenset et al. 2016, De Cuyper et al. 2023). Additionally, we used 14 hour foraging in our model, and although this is mentioned as a realistic foraging time for brown bears in Sweden (Stelmock and Dean 1986), it does not differentiate between walking and eating, hence applying this to the '30 g of berries per minute'-estimate reported by (Welch et al. 1997), might overestimate protein intake. Taking on a more conservative approach of a 10 hour-foraging period leads to a protein intake of 0.14 kg/day (2.23 g/kg$^{0.75}$/day) instead of 0.20 kg/day (3.18 g/kg$^{0.75}$/day), again leaving this model calculation as the only case where brown bears might undershoot domestic dog minimum protein requirements. Finally, one must acknowledge that our approach did not look into the amino acid profile and protein quality of the protein provided by berries or any of the experimental diets used in the captivity studies. The study of amino acid balance and protein quality of plant vs animal protein (McCusker et al. 2014, Golder et al. 2020) can be considered in future research on protein intake and health. This exercise, however, was done to underline where some of the reasoning pitfalls lay in current macronutrient profiling of free-ranging species and to stress the importance of biomass intake. Our hypothetical berry-binging diets remain the only ones so far that actually lead to a protein intake of bears very close to, and – when considering the low protein digestibility in berries – even below domestic dog minimum requirements. Thus, for a short period during autumn berry hyperphagia, brown bears might actually ingest comparatively low amounts of protein that would merit the moniker 'low protein specialist'. However, for other combinations of diet items (cf. Table 1), this was not the case. How the biomass-protein intake relationship manifests itself for other diet items or combination diets typically utilized by bears should still be investigated more profoundly. In many 'bear regions' in autumn, certain resources become very abundant (e.g. fatty nuts, Paralikidis et al. 2010) and bear diets can get rather 'uniform', which would allow similar calculations in the future.

Regardless of the finding that bears self-select for lower dietary protein levels than domestic dogs, dietary protein concentrations for free-ranging brown bears often fall above the average 19–22% DM – 17–21% ME threshold (Coogan et al. 2018, De Cuyper et al. 2023). It is important not to interpret self-selected nutrient levels as a 'requirement'; the self-selected protein level of domestic dogs (30% of ME) is distinctively higher than the experiment-based requirement value of 8–10% (NRC 2006). Methods such as the geometric framework are based on proportions rather than absolute intakes and, therefore, cannot identify the fulfilment of nutrient requirements. Additionally, caution needs to be applied when comparing data from different self-selecting studies if diets of different combinations of macronutrients were used. Should it be corroborated that domestic dogs self-select for higher protein diets than bears when bears are not hyperphagic, rather than being an indication for a lower protein requirement of bears, this might indicate a limited capacity of bears to handle surplus protein. To date, existing data does not allow a reasonable speculation.

In conclusion, a careful consideration of biomass intake next to the macronutrient profile of the ingested diet should be standardized in the study of macronutrient profiling.

Significance statement

This paper evaluates the effect of including absolute biomass intake in the interpretation of dietary macronutrient profiles of brown bears and shows how influential this can be. It gives more insight into how basic nutrition principles should be considered in the nutritional ecology of nondomestic species. The results indicate that even when consuming diets of low protein content, hyperphagic bears ingest protein in amounts that exceed the protein requirements for domestic dogs or cats, suggesting that the label low-protein-specialist for bears might give rise to misconceptions.

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Author contributions

Annelies De Cuyper: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Geert P. J. Janssens**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Visualization (equal); Writing – review and editing (equal). **Marcus Clauss**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Supervision (equal); Visualization (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.bnzs7h4nk (De Cuyper et al. 2025).

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