

ARTICLE

Testing foraging optimization models in brown bears: Time for a paradigm shift in nutritional ecology?

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Abstract

How organisms obtain energy to survive and reproduce is fundamental to ecology, yet researchers use theoretical concepts represented by simplified models to estimate diet and predict community interactions. Such simplistic models can sometimes limit our understanding of ecological principles. We used a polyphagous species with a wide distribution, the brown bear (*Ursus arctos*), to illustrate how disparate theoretical frameworks in ecology can affect conclusions regarding ecological communities. We used stable isotope measurements ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) from hairs of individually monitored bears in Sweden and Bayesian mixing models to estimate dietary proportions of ants, moose, and three berry species to compare with other brown bear populations. We also developed three hypotheses based on predominant foraging literature, and then compared predicted diets to field estimates. Our three models assumed (1) bears forage to optimize caloric efficiency (optimum foraging model), predicting bears predominately eat berries (~70% of diet) and opportunistically feed on moose (*Alces alces*) and ants (*Formica* spp. and *Camponotus* spp; ~15% each); (2) bears maximize meat intake (maximizing fitness model), predicting a diet of 35%–50% moose, followed by ants (~30%), and berries (~15%); (3) bears forage to optimize macronutrient balance (macronutrient model), predicting a diet of ~22% (dry weight) or 17% metabolizable energy from proteins, with the rest made up of carbohydrates and lipids (~49% and 29% dry matter or 53% and 30% metabolizable energy, respectively). Bears primarily consumed bilberries (*Vaccinium myrtillus*; 50%–55%), followed by lingonberries (*V. vitis-idaea*; 22%–30%), crowberries (*Empetrum nigrum*; 8%–15%), ants (5%–8%), and moose (3%–4%). Dry matter dietary protein was lower than predicted by the maximizing fitness model and the macronutrient balancing model, but protein made up a larger proportion of the metabolizable energy than predicted. While diets most closely resembled predictions from optimal foraging theory, none of the foraging hypotheses fully described the relationship between foraging and ecological niches in brown bears. Acknowledging

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and broadening models based on foraging theories is more likely to foster novel discoveries and insights into the role of polyphagous species in ecosystems and we encourage this approach.

KEYWORDS

brown bear, diet, foraging theory, macronutrients, omnivore, stable isotopes, *Ursus arctos*

INTRODUCTION

Many ecological principles are built on theoretical relationships connecting diet, space use, and fitness (Darwin, 1839; MacArthur & Pianka, 1966). However, determining such relationships in practice is complicated, as fitness is a complex function of both physiological and environmental constraints that vary among individuals and populations, while diet varies seasonally, across life-history stages, and among individuals. Researchers are typically forced to use imperfect models with specific assumptions and mathematical constraints to test, interpret, and predict ecological community structure and interactions (Evans et al., 2013; Stearns, 2000). Thus, our understanding of a species' ecological niche, from theoretical underpinnings to conclusions drawn, is affected by assumptions and biases. Most foraging models use mathematical optimization theory, which not only has a suite of assumptions, but changing optimization targets leads to different predicted diets, which may alter predicted landscape use and, ultimately, expectations about an organism's ecological niche (Garay et al., 2012; Houston & McNamara, 2014). For instance, researchers from different ecological disciplines typically concentrate on specific aspects of foraging strategies that can lead to distinct, narrow conclusions (Houston & McNamara, 2014). While physiologists may estimate the health implications of nutritionally imbalanced diets (Erlenbach et al., 2014), evolutionary biologists concentrate on ways animals forage to maximize reproductive output (Hilderbrand et al., 1999), and general optimal foraging theory uses energetic (typically caloric) efficiency to explain foraging decisions (MacArthur & Pianka, 1966). When considering diet optimization, a physiologist may require food to be available *ad libitum* to determine the baseline nutritional needs of a species, while a behavioral ecologist is likely to assume that organisms exist in patchy environments in which optimized diets can only be realized under the constraints of a natural environment.

Shifting targets of how we quantify animal foraging and the corresponding inferences that result make a broad ecological understanding of ecological communities difficult. This is particularly true for species with large distributions or which use diverse resources, such as polyphagous species (Loxdale & Harvey, 2023;

Richmond et al., 2005). Brown bears (*Ursus arctos*) have a large circumpolar distribution and use a variety of landscapes and foods (Bojarska & Selva, 2012; Diserens et al., 2020). Although, taxonomically, brown bears are carnivores, most populations consume little meat, relying on vegetation, hard and soft mast, and invertebrates (Bojarska & Selva, 2012; Diserens et al., 2020). However, meat is the most efficiently digested food in brown bear diets (Pritchard & Robbins, 1990) and greater carnivory in brown bears is positively associated with population density, body size, and reproductive output (Hilderbrand et al., 1999; Mowat & Heard, 2006; Zedrosser et al., 2006), partially due to greater fixed nitrogen and energy density at higher trophic levels (Elser et al., 2000). Thus, carnivory is generally assumed to be the ideal foraging niche for brown bears, (Costello et al., 2016; Erlenbach et al., 2014; Hilderbrand et al., 1999; López-Alfaro et al., 2015; Mowat & Heard, 2006). Yet, the variability of brown bear foraging makes it difficult to draw broad conclusions between diet, body size, and fitness, as some populations of brown bears maintain high reproductive output despite small body sizes and relatively low carnivory (Zedrosser et al., 2011). For this reason, we prefer the term polyphagous to carnivore or omnivore (Loxdale & Harvey, 2023).

Much of the theory on the brown bear diet comes from North American coastal populations with access to salmon, which is high in fat and may confound the relationship between meat and fitness (Gende et al., 2001; Hilderbrand et al., 1999; López-Alfaro et al., 2015; Mowat & Heard, 2006). In contrast, brown bears in Sweden feed predominately on moose (*Alces alces*), ants (*Formica* spp. and *Camponotus* spp.), and berries (primarily *Vaccinium* and *Empetrum* species), but the proportions of each diet component vary both seasonally and annually (Dahle et al., 1998; Persson et al., 2001; Stenset et al., 2016). Sweden has one of the highest moose densities in the world and moose are heavily harvested (Jensen et al., 2020), creating many opportunities for bears to scavenge moose carcasses and prey on calves in the spring (Rauset et al., 2012; Stenset et al., 2016; Swenson et al., 2007). In summer, brown bears become largely frugivorous (Dahle et al., 1998; Persson et al., 2001; Stenset et al., 2016) and, although they are patchily

distributed, berries in Scandinavian forests are numerous (Bohlin et al., 2021), providing a predictable food source (Hertel et al., 2016, 2018; Stenset et al., 2016). Throughout their active season, bears also consume ants, but foraging peaks in mid-summer after the moose calving season, but before berries are widely available (Stenset et al., 2016). Ants are abundant in Sweden (Frank et al., 2015; Swenson et al., 1999), but the numbers of pupae vary seasonally, changing the overall caloric value of ants as food (Swenson et al., 1999).

Brown bears in Sweden have a reproductive output associated with a diet of ~77% meat (Hilderbrand et al., 1999; McLellan, 2011; Zedrosser et al., 2011), which would be twice the meat consumption estimated previously (Dahle et al., 1998; Persson et al., 2001; Stenset et al., 2016). Assuming that bears maximize meat intake to maximize reproductive output (maximizing fitness model), bears should predominately consume vulnerable moose calves in the spring and scavenge moose carcasses whenever available, and then bears should favor ants to maintain protein and energy intake (Hilderbrand et al., 1999; Mowat & Heard, 2006), while berries should be consumed minimally (Coogan et al., 2014; Erlenbach et al., 2014). Under the maximizing fitness model, bears should be major predators of the vertebrate community, minimally interact with the plant community, and be sensitive to future changes in prey populations.

In contrast with maximizing meat consumption, many foraging models use overall caloric efficiency as the diet component to be optimized (optimum foraging model), which predicts that bears in Sweden should favor foraging on berries over moose. Scandinavia's history of intensive silviculture (Östlund et al., 1997) has created a landscape in which berries are abundant, while moose and ants are distributed more sporadically across the landscape (Rauset et al., 2012; Swenson et al., 1999). Berries are less digestible and less energy dense than ants and moose (3.04 kcal/g vs. 4.77 and 5.13 kcal/g, respectively), yet their availability and ease of capture relative to moose and ants make them more energetically economical and therefore, the best food source (MacArthur & Pianka, 1966). The optimum foraging model predicts brown bears to be minor predators of vertebrates and ants (probably only opportunistically) and strong interactions with the plant community, probably sensitive to changes in berry production.

Rather than assume an organism seeks to optimize a single currency, such as caloric efficiency or meat, organisms may forage to balance multiple currencies (Coogan et al., 2014; Erlenbach et al., 2014; Houston & McNamara, 2014) such as an ideal macronutrient ratio (balancing macronutrient model; Erlenbach et al., 2014; Raubenheimer et al., 2009). Feeding experiments offer a way to specifically measure the ratio of macronutrients

animals prefer, and captive brown bears select a diet of approximately 22% dry matter protein, 17% metabolizable energy content from protein, and 78% dry matter or 70% energy from nonprotein sources, with bears preferring lipids over carbohydrates (Erlenbach et al., 2014). Food that provides predominately one macronutrient, such as berries and moose meat, are low-quality foods whereas, ants, which offer more balanced ratios of proteins, carbohydrates, and lipids, are of higher quality (Raubenheimer et al., 2009; Appendix S1: Table S1). Under the balancing macronutrient model, bears should predominantly consume ants and, to a lesser extent, moose to meet protein demands and then use berries to meet energetic demands while avoiding protein overconsumption (Erlenbach et al., 2014; Robbins et al., 2022; Rode et al., 2021). This model predicts that brown bears are major predators of ants, minor predators of moose, and moderately interact with the plant community.

In addition to biases imposed by assumptions associated with chosen foraging targets and model constraints, field methods to estimate diets, such as observation, scat and gut content analyses, or cafeteria-style feeding experiments, also have inherent biases and assumptions that can affect results and inferences (Tieszen & Boutton, 1989). Furthermore, many of these methods cannot explain how organisms assimilate ingested foods into new tissues (Tieszen & Boutton, 1989). A carnivore or polyphagous species may regularly ingest plants, but an important distinction is whether this is done to aid gut transit or build new tissues (Leigh et al., 2018). Naturally occurring stable isotope values of tissues are related to the assimilated diet and can be used to estimate the proportions of isotopically unique foods used by animals (Chamberlain et al., 2005; Felicetti et al., 2003; Koehler et al., 2019; Tieszen & Boutton, 1989).

A clear understanding of an organism's foraging behavior is essential to defining ecological interactions, while understanding energy allocation is vital to describing life history and how animals respond to future environmental perturbations or long-term changes. The goal of this study was to use stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) measurements to estimate dietary proportions of five foods in the brown bear diet and to compare these estimates to those reported in earlier conventional (i.e., scat analyses) studies on the same population. We also aimed to compare the diet of bears in southcentral Sweden to other populations throughout their range. Brown bears were also used as a model species to illustrate how theoretical assumptions, model constraints, and different optimization targets result in different predicted diets, as well as ecological niches. We used published papers on brown bear ecology from across their range (Bojarska & Selva, 2012; Craighead & Mitchell, 1982; Hilderbrand et al.,

1999; Jacoby et al., 1999; Pritchard & Robbins, 1990; Stenset et al., 2016; Swenson et al., 1999; Zedrosser et al., 2006, 2011) to develop three foraging hypotheses within the framework of optimal foraging, maximizing fitness, and balancing macronutrients. We then compared the predicted diet to the observed estimated diet to determine how well foraging theories described the behavior of wild populations. Assuming bears forage to maximize fitness, meat should make up 35%–50% of their diet, with ants and berries making up the rest (~30% and ~15% respectively). Under the optimal foraging model, bears should predominantly consume berries (~70%) and opportunistically feed on moose and ants (~15% each). Finally, under the balancing macronutrients model, bears will have mixed diets that will vary in food sources but result in ~22% protein and 78% nonprotein sources, with more lipids than carbohydrates (Figure 1).

MATERIALS AND METHODS

Our study area encompassed ~13,000 km² in Gävleborg and Dalarna counties in southcentral Sweden with low

human density and heavily managed forests of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Hair samples were collected by plucking with pliers from a standardized location between the shoulders (hump) of brown bears during spring captures of a wild population monitored by the Scandinavian Brown Bear Research Project. Bears were captured by darting with an immobilizing drug from a helicopter (Arnemo & Evans, 2017) in spring soon after den emergence (March through May). All capture procedures were conducted in accordance with the Swedish Environmental Protection Agency, Swedish Board of Agriculture, and Swedish Ethical Committee on Animal Research (Uppsala Djurförsöksetiska Nämnd: C40/3, C212/9, C47/9, C210/10, C7/12, C268/12, C18/15. Statens Veterinärmediciniska Anstalt, Jordbruksverket, Naturvårdsverket: Dnr 35-846/03, Dnr 412-7093-08 NV, Dnr 412-7327-09 Nv, Dnr 31-11102/12, NV-01758-14). After collection, hair samples were placed in individual paper envelopes and stored dry at room temperature.

In brown bears, hair growth begins in late April and continues into October, with a quiescent phase over winter, but the actual growth phase varies by individual (Cattet et al., 2018; Jacoby et al., 1999; Jimbo et al., 2020).

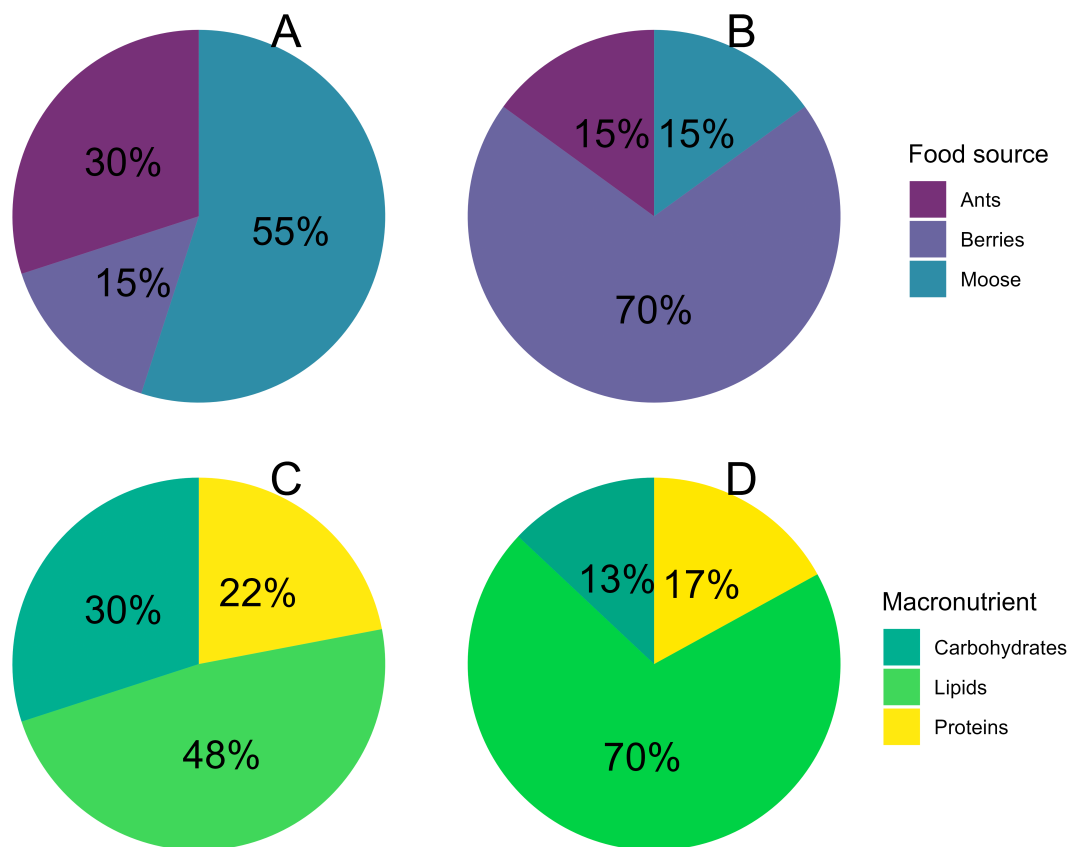


FIGURE 1 Pie charts representing the predicted diet of brown bears in southcentral Sweden sampled 1995–2015 with three different foraging currencies: maximizing fitness (A), optimum foraging (B), macronutrient balance (% dry matter) (C), and macronutrient balance (% metabolizable energy) (D).

Bears in this study were captured in the spring and we used many homogenized guard hairs, thus collected hair samples represented diet from the entire previous active season, from the moose calving to berry season (Dahle et al., 1998; Persson et al., 2001; Rode et al., 2016; Stenset et al., 2016). While hair is a protein-based tissue, carbon in hair can be derived from all sources within the diet.

When processing brown bear hair, we only used guard hairs and removed visible surface contaminants, then weighed hairs to the nearest milligram. Preparatory procedures followed the protocol for cortisol concentration measurement (Macbeth et al., 2010) and samples for stable isotope assay were portioned out after the grinding step (Sergiel et al., 2017; Appendix S1). We washed each sample three times with 40 μ L HPLC grade methanol per mg hair for 3 min per wash to remove other external contaminants (Sergiel et al., 2020). After the hair had dried for at least 24 h, it was ground to a fine powder in a mixer mill (Retsch MM4000; Retsch GmbH, Germany) at 30 Hz and then put into plastic vials. To measure $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in hair, we followed Koehler et al. (2019) and weighed 1 mg of powdered (treated) hair into precombusted tin capsules. Encapsulated hair was combusted at 1030°C in a Carlo Erba NA1500 or Eurovector 3000 elemental analyzer. The resulting N_2 and CO_2 were separated chromatographically and introduced to an Elementar Isoprime or a Nu Instruments Horizon isotope ratio mass spectrometer. We used two reference materials to normalize the results to VPDB and AIR: BWBIII keratin ($\delta^{13}\text{C} = -20.18\text{‰}$, $\delta^{15}\text{N} = +14.31\text{‰}$, respectively) and PRCgel ($\delta^{13}\text{C} = -13.64\text{‰}$, $\delta^{15}\text{N} = +5.07\text{‰}$, respectively). Within run ($n = 5$) precisions as determined from both reference and sample duplicate analyses and from QA/QC controls were $\pm 0.1\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

To estimate dietary proportions, we used stable isotope values from the five main bear foods in the study area: bilberry (*Vaccinium myrtillus*), crowberry (*Empetrum nigrum*), lingonberry (*Vaccinium vitis-idaea*), ants, and moose. In 2016, berry and ant samples were collected from within the study area. To determine the proportion of moose in the diet, we used moose hairs collected from local wild moose. We used nutritional information from previous bear studies and the USDA National Nutrient Database (Coogan et al., 2014; Erlenbach et al., 2014; Swenson et al., 1999; U. S. Department of Agriculture, Agricultural Research Service, 2018) to estimate the percent protein, carbohydrates, and fat in brown bear diets (Appendix S1: Table S1).

Prior to analysis, we corrected $\delta^{13}\text{C}$ values for the anthropogenic depletion of ^{13}C in the atmosphere caused by fossil fuel combustion (Seuss effect) by applying a -0.022‰ correction per year (Chamberlain et al., 2005) and derived source-specific trophic discrimination factors to convert prey $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to hair equivalent

values (Appendix S1). Then, we graphed our consumers and food sources in isotopic bivariate space to ensure that bears in our study fell within the mixing polygon and that each endpoint was isotopically distinct (Figure 2; Phillips et al., 2014). Based on the isotopic mixing space (Figure 2) the ant and moose dietary endpoints were isotopically similar, as were those of crowberry and lingonberry, indicating that the model was unable to distinguish between them. However, we decided to group end members *a posteriori* rather than *a priori* (Parnell et al., 2013; Phillips et al., 2014). For final diet estimations, we used the package *simmr* (Parnell et al., 2013) in R (R Core Team, 2022) with uninformative priors (Appendix S1: Table S4) and four chains for 1,000,000 iterations, a burn-in of 500,000, and a thinning rate of 500. Initial values were randomly generated. We accounted for concentration dependency in the model by including the percent carbon and nitrogen of each food source (Phillips & Koch, 2002; Appendix S1: Table S5).

Following Erlenbach et al. (2014) and Coogan et al. (2014), we used the posterior mean dietary proportions calculated from the mixing models and published macronutrient contents for each food group (ants, berries, and moose) to calculate the percent dry matter and percent metabolizable energy of lipids, proteins, and carbohydrates in the diet (Appendix S1: Tables S1 and S7).

RESULTS

We analyzed hair samples from 378 individuals collected during 1995–2015. Our data contained 840 unique bear-year combinations (Appendix S1: Table S6) to estimate dietary proportions of the five main foods for brown bears in southcentral Sweden. After the application of trophic discrimination factors and accounting for concentration dependence, the model partially differentiated between the ant and moose endpoints, as well as the three berry endpoints. Ants and moose estimates had a correlation of -0.74 , while crowberry and lingonberry had a correlation of -0.79 . A negative correlation among source estimates indicates that the sources were too similar to be confidently estimated separately and increasing the proportion of one food results in a corresponding decrease of the negatively correlated source. For example, given the error around the estimates of ants and moose, there was evidence that ants made up a greater proportion than moose, but the exact proportion of the two correlated foods could not be precisely determined. However, the resulting diet estimates did not overlap (Figure 3) and, although we calculated separate berry proportions, when deriving inferences, berries were considered as a single category, therefore we did not combine diet sources *a priori*.

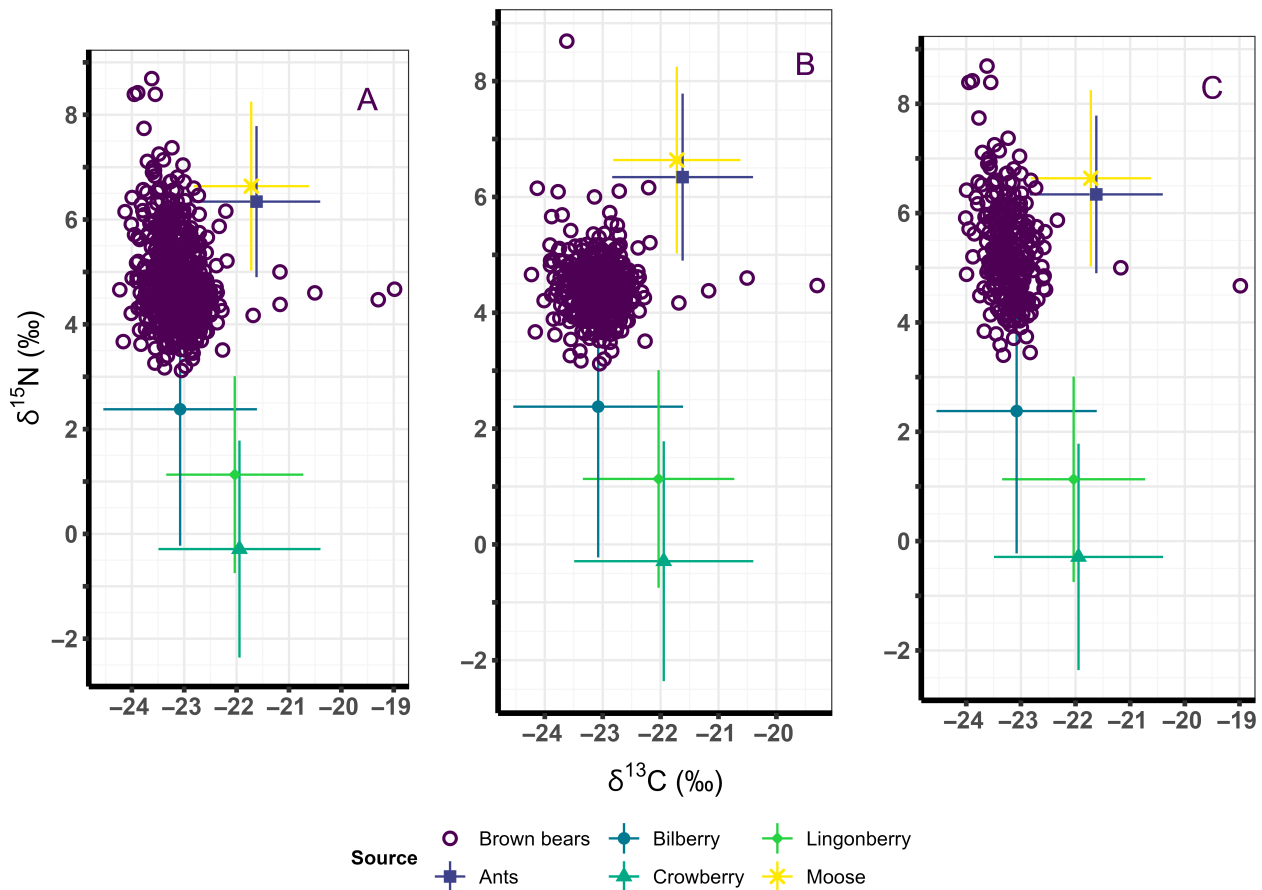


FIGURE 2 Biplot of carbon and nitrogen isotope values from individual brown bears across the entire population (A), for independent females only (B), and independent males only (C) sampled in southcentral Sweden 1995–2015. Mean values and standard errors of each of the five dietary endpoints representing the predicted isotope signature of a bear consuming 100% of each food type. Dietary endpoints have been corrected with trophic enrichment factors to represent a bear consuming 100% of that diet.

Bears in our population primarily consumed bilberries (50%–55%), followed by lingonberries (22%–30%), crowberries (8%–15%), ants (5%–8%), and moose (3%–4%; Figure 3). Among berry species, dietary proportions mirrored nitrogen content, with bilberry having the greatest nitrogen content (0.81%) followed by lingonberry (0.64%), and crowberry with the lowest nitrogen content (0.42%; Appendix S1: Tables S1 and S6).

When we considered the percent dry matter macronutrient proportions and percent metabolizable energy, proteins in the diet were well below predictions from the maximizing fitness model (~13% observed vs. ~40%–50% predicted) and less than predicted by the balancing macronutrients model (predicted: 22% dry matter and 17% metabolizable energy, observed: 13% dry matter and 12% metabolizable energy; Table 1). Although berries are low in proteins, due to their large proportion of the diet, they are the largest source of protein. The observed brown bear diet was also lower in lipids than predicted by the balancing macronutrients model.

DISCUSSION

Diet and resource acquisition have long been standard measures for understanding behavior, survival, reproduction, community interactions, and evolution (Darwin, 1839; MacArthur & Pianka, 1966). We used brown bears to illustrate that even within a well studied species, the application of models that use different foraging targets or strategies can result in different predicted diets, behaviors, and niches, which affects our fundamental understanding of ecology. Our results using a simple bulk stable-carbon and nitrogen isotope analysis indicate that bears in our study ate less proteins, fats, and meat than predicted. This finding differs from accepted life history theory in this species, specifically, the relationship between carnivory, body size, and reproductive output. More specific studies that analyze a larger suite of elements or use specific amino acids might be able to differentiate between bulk foods that were isotopically similar in this system (Whiteman et al., 2019). That approach may provide a more precise understanding of metabolic

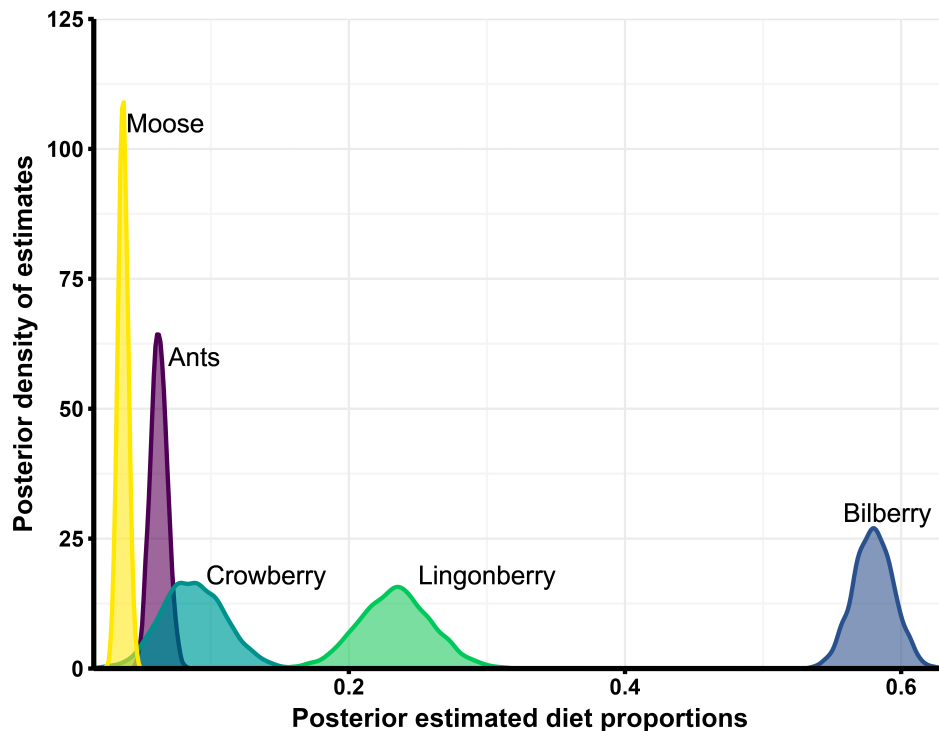


FIGURE 3 Density plot of posterior distributions of the dietary proportions calculated from Bayesian mixing models of proportions of hair $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from brown bears sampled 1995–2015 in southcentral Sweden.

routing. In addition, our results emphasize areas within foraging ecology that could be improved to further our understanding of basic ecology. Many of the ecological and mathematical assumptions within our models may have limited the scope and depth of ecological inferences. Below, we highlight some of these limitations and proposed modifications.

Our estimated brown bear diets were lower in meat and protein than predicted under the maximizing fitness or balancing macronutrients model. Diet greater than one-third meat, as estimated from previous scat analyses, would indicate that brown bears were consuming protein quantities more like obligate carnivores, such as felids, rather than other polyphagous species (Clauss et al., 2010). Protein overconsumption is linked to kidney and liver disease, as well as an increased risk of cancer (Delimaris, 2013; Robbins et al., 2022; Rode et al., 2021). One issue related to estimating protein in diets of wild animals is that estimates often cannot differentiate between skeletal muscle, which is high in protein and deficient in fats and carbohydrates, and viscera, which has a more balanced macronutrient content (U. S. Department of Agriculture, Agricultural Research Service, 2018). Often, both skeletal muscle and viscera are collectively referred to as “meat” (Felicetti et al., 2003; Hilderbrand et al., 1996; Hobson et al., 2000; Mizukami et al., 2005),

despite their macronutrient differences and a consumer’s ability to preferentially consume one over the other (Gende et al., 2001; Towner et al., 2022).

Predictions from the optimal foraging model best resembled estimates from stable isotope analysis of hair whereby berries constituted most of the diet (~89%) while ants and moose made up small proportions during hair growth (~7% and 4%, respectively). Even combined as a single nitrogen source, moose and ants account for $11\% \pm 0.3\%$ of the diet, indicating that nitrogen-rich foods made up a small portion of the energy budget. From these results, we might conclude that brown bears in southcentral Sweden are weak predators of moose, given that moose make up only a small portion of the brown bear diet. Yet bears prey on a large proportion of moose calves born annually (~25%; Rauset et al., 2012; Swenson et al., 2007), and thus the optimum foraging model is likely to underestimate the interaction between moose and brown bears. Brown bear predation on moose varies by individual (Rauset et al., 2012; Swenson et al., 2007), which was also indicated in the variation of hair $\delta^{15}\text{N}$ values within our population (Appendix S1; Figure 1). Thus, we do not expect all predators to exert uniform predation pressure on their prey, nor do we expect all predators to respond uniformly to changes in a given prey population (Bolnick et al., 2003).

Based solely on the isotopic analysis of hair, our study could not account for individual variation or seasonal

TABLE 1 Dietary proportions of three macromolecules calculated from the mean posterior estimates of dietary proportions calculated from Bayesian mixing models of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ hair values of brown bears sampled 1995–2015 in southcentral Sweden.

Food source	Estimated diet proportion	Proteins	Carbohydrates	Lipids	Total energy
Macromolecule proportions ^a					
Moose	4.0	68.6	2.6	24.1	
Ants	7.0	39.5	17.8	26.6	
Berries	89.0	4.8	63.8	3.9	
Macronutrient metabolic conversion factors ^b					
Moose	4.0	4.27	0.95	9.02	5.13 ^c
Ants	7.0	4.27	3.87	9.02	4.77 ^c
Berries	89.0	3.36	4.00	8.37	3.04 ^c
Macronutrient percent dry matter contribution to diet ^c					
Moose	4.0	0.027	0.001	0.010	
Ants	7.0	0.028	0.012	0.019	
Berries	89.0	0.043	0.568	0.034	
Absolute value	100.0	0.10	0.58	0.06	0.74
Diet proportion		0.13	0.78	0.08	
Macronutrient percent energy contribution to diet ^d					
Moose	4.0	0.12	0.00	0.09	0.21 ^f
Ants	7.0	0.12	0.05	0.17	0.33 ^f
Berries	89.0	0.14	2.27	0.29	2.70 ^f
Total energy per macronutrient ^g		0.38	2.32	0.54	3.24

Note: Results are reported in percent dry matter as well as percent metabolizable energy of the whole diet.

^aMacromolecule proportions (% dry matter) were calculated from previously published literature on brown bears as well as information published by United States Department of Agriculture (Coogan et al., 2014; Erlenbach et al., 2014; Swenson et al., 1999; U. S. Department of Agriculture, Agricultural Research Service, 2018).

^bMetabolizable energy calculated using Atwater specific factors (Merrill & Watt, 1973).

^cMacronutrient absolute value dry matter in diet = $\sum \% \text{Macronutrient}_{j(\text{source}_i)} \times \% \text{diet}_{(\text{source}_i)}$ and Diet proportion = $\frac{\sum \% \text{Macronutrient}_{j(\text{source}_i)} \times \% \text{diet}_{(\text{source}_i)}}{\sum \text{Absolute values}}$.

^dDiet specific macronutrient contribution (kcal/g) = $\sum \% \text{Macronutrient}_{j(\text{source}_i)} \times \text{metabolic conversion factor}_{(\text{source}_i)} \times \% \text{diet}_{(\text{source}_i)}$.

^eTotal energy (in kilocalories per gram).

^fTotal energy per food (in kilocalories per gram).

^gTotal energy per macronutrient (in kilocalories per gram).

changes in diet. Bear hair grows from late April to October, but growing periods vary considerably (Cattet et al., 2018; Jacoby et al., 1999; Jimbo et al., 2020), and hair is not a completely inert tissue. Bears in our study tend to consume more protein-rich foods during the breeding season (May–July), which coincides with the moose calving season, but during this time bears spend little time foraging (Stenset et al., 2016; Swenson et al., 2007). This variation in seasonal diets by bears presents a challenge to inferences derived from any method used to estimate diets, unless researchers use repeated sampling or a suite of tissues representing different periods of dietary integration. Hair overwhelmingly represents a protein metabolic pathway (i.e., all nitrogen in hair is derived from proteins in diet or body tissue and not from lipids or carbohydrates). However, carbon in hair can be derived from all three macronutrients. We

attempted to account for macromolecular compositions of diets based on a largely protein-based mixing model (in turn dependent on $\delta^{15}\text{N}$ measurements in the mixing model) and our isotopic discrimination factors were specific to both plant and animal diets. In addition, the exact proportions of each food in the diet could not be precisely estimated in our analysis, because the moose and ant end members had similar isotopic signatures. Moose and ant endpoints were negatively correlated (-0.74), yet this alone does not make our results uninformative (Parnell et al., 2013). While we did not determine the dietary proportions of ants versus moose, it is clear from the posterior distribution that ants made up a larger proportion of the diet than moose (Figure 3). Given the narrow range of estimates (ants: 5%–8%, moose: 3%–4%) and low variation (ants SD = 0.06%, moose SD = 0.04%), even assuming the highest proportion of moose (12% of diet with 0% ants) the

overall percent dry matter content of protein only increased by ~3%. A diet of 12% moose and 0% ants is still much lower in protein than predicted from captive feeding trials (16%–28% predicted dry matter protein content vs. ~12.5% observed and 13%–21% predicted percent energetic content of protein vs. ~11.5% observed). Thus, our conclusions regarding brown bear foraging targets and the effects of model assumptions remained unchanged, despite isotopic similarities between these two food types.

Our understanding of animal diet and foraging ecology remains incomplete, due in part to biases within our theoretical and methodological frameworks (Mougi & Nishimura, 2008; Stearns, 2000). For instance, within community ecology, until recently models have neglected polyphagous species (Thompson et al., 2007), assuming they are rare, destabilizing members of food webs (Chubaty et al., 2014; Gutgesell et al., 2022). This assumption biased early research into categorizing species within a fixed dichotomy of carnivory versus herbivory separated by discrete trophic levels (Chubaty et al., 2014). However, polyphagy is prevalent in varying degrees across taxa, trophic levels, and ecosystems (Chubaty et al., 2014; Thompson et al., 2007). Models that relax the foundational ecological assumptions, such as carnivore–herbivore dichotomies, fixed trophic levels, stable equilibria, and organisms as perfect consumers, can explain realized, complex ecological communities better than simplified, rigid models (Mougi & Nishimura, 2008; Stearns, 2000).

Even though modern nutritional ecology models use macronutrient balance as their optimization targets (Coogan et al., 2014; Raubenheimer et al., 2009; Rode et al., 2021), determining “optimal” macronutrient balance often comes from cafeteria-style feeding experiments in laboratory or zoo settings (Erlenbach et al., 2014; Felicetti et al., 2003). These studies may have limited application to wild populations because they do not account for search and handling time or changing availability on the landscape. Macronutrient content of wild brown bear diets differed from predictions from captive feeding trials, which is likely related to the search and handling time of high-protein foods in our system and inherently different metabolic demands for free-ranging bears, rather than evidence that macronutrient balance is not important to brown bears. Berries are also assumed to be low in lipids, yet many species, including two in this study, are rich in fatty acids (Klavins et al., 2019). Therefore, moose offal and berries may contribute more lipids than we estimated.

Diets of Scandinavian brown bears contained less meat and protein than predicted from the maximizing fitness and balancing macronutrient models. Even though annual diets most closely resembled predictions from the optimum foraging model, none of the three models fully described the relationship between foraging and

community interactions in our system. In general, herbivorous diets may not be as protein limited as historically thought and overconsuming protein has negative health consequences for polyphagous species (Robbins et al., 2022; Rode et al., 2021; Rothman et al., 2011). Life histories are aggregates of complex interactions between energy acquisition and allocation, macronutrient balance, and nutrient limitations to which different species, populations, and even individuals within populations have adapted. Acknowledging and broadening foraging theories are more likely to foster novel discoveries and insights into ecosystems than constraining behavior to anthropogenically imposed categories and assumptions. Future studies should carefully consider the explicit and implicit assumptions contained in theories and models that we apply to ecological studies and loosen assumptions to accommodate the dynamic and cryptic relationships often missed in narrow ecological studies.

AUTHOR CONTRIBUTIONS

Nuria Selva and Andreas Zedrosser conceived the ideas and designed the methodology. Keith A. Hobson, Agnieszka Sergiel, and Ashlee J. Mikkelsen performed laboratory protocols. Ashlee J. Mikkelsen analyzed the data. Ashlee J. Mikkelsen, Anne G. Hertel, and Andreas Zedrosser led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Mikkelsen, 2023) are available in the University of South-Eastern Norway Research Data Archive at <https://doi.org/10.23642/usn.24492169.v1>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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