

Might macronutrient requirements influence grizzly bear–human conflict? Insights from nutritional geometry

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Abstract. Knowledge of carnivore nutritional requirements offers a potentially powerful aid for conservation and management strategies, yet has received little attention. We discuss how nutritional ecology, nutritional geometry, and the concept of macronutrient (protein, lipid, and carbohydrate) balance can be used to further our understanding of behavioral regulatory mechanisms that may influence food-related human–wildlife conflict, focusing on North American grizzly bears (*Ursus arctos*). We propose that the macronutrient preferences of omnivorous grizzly bears are a strong driver of their conflict with humans due to nutrient-specific foraging behavior, which we predict will be particularly noticeable during periods in which “key” natural foods high in lipid or carbohydrate are limiting. We demonstrate how nutritional geometry can be used to investigate the concept of nutrient balance by integrating recent research on the macronutrient selection of the grizzly bear with nutritional estimates of potentially consumed anthropogenic foods. Our geometric analysis utilizing right-angled mixture triangles suggested that anthropogenic foods offer grizzly bears nonprotein energy sources that may allow them to optimize macronutrient intake. This macronutrient-focused approach gives rise to fundamentally different predictions (and potentially management strategies) than the conventional food and energy-focused approaches. This article also provides insight into food-related conflict among other bear and carnivore species, and human–carnivore conflict more generally, by outlining a nutritionally explicit predictive framework for understanding the potentially volatile interface between anthropogenic environments and the behavior of wild animals.

Key words: brown bear; carbohydrate; fat; garbage; grizzly bear; human–wildlife conflict; lipid; macronutrients; nutritional ecology; nutritional geometry; right-angled mixture triangle; *Ursus arctos*.

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INTRODUCTION

Conflict between carnivores (order Carnivora) and humans is an issue of global concern (Trevés and Karanth 2003, Chapron et al. 2014, Ripple et al. 2014). Managing such conflict, which often arises through competition for food resources, is challenging (Can et al. 2014, Boitani et al. 2015).

Carnivores found in close proximity to humans and in urban areas are regularly considered “problem wildlife” and often consume anthropogenic foods (Gunther et al. 2004, Bino et al. 2010, Northrup et al. 2012, Elfström et al. 2014a, Murray et al. 2015). Livestock depredation by carnivores can result in large financial losses and retaliatory killing, which in turn may fuel negative

perceptions and persecution of large predators by humans (Kellert et al. 2002, Treves and Karanth 2003, Zedrosser et al. 2011, Aryal et al. 2014). The need to understand the underlying biology and design effective management strategies for animals involved in food-based conflict is therefore an imperative for wildlife conservation.

Perhaps no group of animals is better known for potential food-related conflict with humans than bears (Ursidae). The grizzly bear (or brown bear outside North America; *Ursus arctos*) is an omnivorous carnivore with a diverse and opportunistic diet (Bojarska and Selva 2011, Edwards et al. 2011, López-Alfaro et al. 2015) which allows them to feed on a wide variety of foods both in the wild and also associated with humans. Across their distribution, grizzly bears enter into conflict with humans in incidences related to anthropogenic foods (Can et al. 2014). Food-related grizzly bear-human conflict is generally more pronounced in North America than in Europe (Elfström et al. 2014b) and other areas (Can et al. 2014). Food search may be the primary reason grizzly bears approach human settlements in North America (Herrero et al. 2005, Elfström et al. 2014b), possibly because these populations often inhabit less productive ecosystems (Bojarska and Selva 2011, Elfström et al. 2014b). In North America, anthropogenic food attractants of grizzly bears include garbage, livestock, crops, grain, orchards, apiaries, domestic gardens, pet food, bird feed, livestock feed, grease, human foods and beverages, and other edible human attractants (Craighead et al. 1995, Gunther et al. 2004, Spencer et al. 2007, Northrup et al. 2012, Hopkins et al. 2014).

Incidences of bear-human conflict in North America are typically highest during the late-summer and fall hyperphagic period (Herrero and Higgins 2003, Gunther et al. 2004, Spencer et al. 2007), a time in which bears prioritize the accumulation of body mass in preparation for winter denning and the female reproductive period (López-Alfaro et al. 2013) and display enhanced insulin sensitivity (Nelson et al. 2015). Additionally, incidences of grizzly bear-human conflict increase substantially when natural food availability is low, especially “key” foods high in lipid or carbohydrate such as seeds and fruit (Mattson et al. 1992, Gunther et al. 2004, Schwartz et al. 2006). Another scenario may emerge in which sub-dominant bears utilize anthropogenic habi-

tats to avoid conflict with, or predation by, conspecifics (Elfström et al. 2014b), and are therefore exposed to a range of anthropogenic foods from which to compose their diet. Whatever the cause, this is not without consequence, as the risk of damage to property, human-caused bear mortality, and bear-caused human injury and mortality, increases when bears obtain anthropogenic foods (Herrero and Higgins 2003, Gunther et al. 2004).

Traditionally, the diet of bears has been examined from an optimal foraging theory (OFT) perspective. Under OFT, patterns of food selection by foraging animals are thought to be optimized by natural selection to maximize fitness (Pyke et al. 1977). Because fitness can be difficult to measure directly, typically a proxy for fitness is used as a focal variable (a fitness “currency”), such as rate of energy gain (assumed to be maximized), time spent in gaining energy (minimized), or predation risk (minimized; Stephens and Krebs 1986). Because OFT most commonly predicts that foragers attempt to maximize their intake of energy (Charnov 1976, Stephens and Krebs 1986, Whelan and Schmidt 2007), many early bear studies have focused on energetic aspects of foraging and consumption rates (e.g., Bunnell and Hamilton 1983, Welch et al. 1997, Rode et al. 2001, Klinka and Reimchen 2002, Wilmers and Stahler 2002). Protein and food digestibility were also often considered in addition to energy in diet studies (Pritchard and Robbins 1990, McLellan and Hovey 1995, Hilderbrand et al. 1999a,b, Munro et al. 2006, Coogan et al. 2012), yet carbohydrate and lipid were mostly overlooked.

While such studies have yielded important insights, accumulation of data on nutritional regulation in animals has called into question the resolution of OFT models for explaining and predicting nutritional behavior (Pierce and Ollason 1987, Raubenheimer and Simpson 1997, Illius et al. 2002, Simpson et al. 2004, Raubenheimer et al. 2009, Jensen et al. 2012). Energy is not in itself a nutrient, but rather is a resource that can be obtained in the form of the macronutrients proteins, fats, and carbohydrates (and, for some animals, fiber). However, the relationships between specific macronutrients and energy provisioning are complex. Animals vary in their ability to utilize energy from fats, carbohydrates, and proteins, and they also require these nutrients for purposes other than energy provisioning (e.g., protein

for muscle growth, fatty acids for membrane synthesis). Models that do not explicitly distinguish among the macronutrients but rather combine them into an overall energy contribution are therefore likely to exclude important functional aspects of an animal's relationship with potential foods and food selection, and might confound energy maximization with behavior directed at acquiring the specific macronutrients in particular ratios (Raubenheimer et al. 2009, Raubenheimer 2011). *A priori*, therefore, it is likely that consideration of specific macronutrients provides a stronger basis for predicting, interpreting, and managing foraging behavior than does energy *per se*.

Recently, researchers have shown that specific macronutrients play a strong role in the diet selection of grizzly bears. Both wild and captive grizzly bears were shown to mix their diet between salmon (Genus: *Oncorhynchus*) and fruit (Robbins et al. 2007), despite energy maximizing theory predicting bears to forage exclusively on more energetically profitable salmon. The relationship between energy, macronutrients, and diet intake was further examined in captive grizzly bears, which were shown to self-select a mixed diet consisting of 17% protein energy to 83% nonprotein (lipid + carbohydrate) energy (% metabolizable energy; Erlenbach et al. 2014). Furthermore, the selected diet maximized their mass gain per unit energy intake, where mass gain was considered a measure of fitness. Bears regulated their protein intake, using lipid and carbohydrate interchangeably as nonprotein energy sources, although lipids were preferred when available (Erlenbach et al. 2014). This relationship between macronutrient balance and diet optimization was then further extended to the field, where the diet quality of a wild bear population in Alberta, Canada, was assessed for its ability to provide an optimal ratio of macronutrients seasonally (Coogan et al. 2014). That study provided insights into the nutritional factors that may limit the population, as well as a nutritional basis for predictive models of bear foraging. From a macronutrient balance perspective, nonprotein energy was limiting to bears in the northern Alberta study area except during hyperphagic periods in which fruit was available (Coogan et al. 2014).

In this article, we propose that the concept of macronutrient balance provides a powerful predictive framework for understanding behavior-

al regulatory mechanisms that may influence food-related grizzly bear-human conflict. We first introduce nutritional geometry and the right-angled mixture triangle (RMT) to demonstrate how the concept of nutrient-specific foraging can inform grizzly bear behavior. We do this by relating recent research on grizzly bear macronutrient preferences with the compositions of key natural foods and various human-related foods that might potentially play a role in bear-human conflict. We demonstrate that it is not the energy content of foods *per se* that will trigger grizzly bear-human conflict during times of shortage of "key" foods, but specifically the relative contribution of energy from nonprotein macronutrients. Foods with similar energy density contributed predominately by protein, such as lean meats, will be less problematic. Under such circumstances, nutritional mismatch between the macronutrient preferences of bears and macronutrients in available foods may have a strong role to play in food-related bear-human conflict through lipid- and carbohydrate-seeking behavior. Furthermore, understanding the concept of macronutrient balance will help explain how bears foraging in different habitats (e.g., wild vs. anthropogenic) may consume a diet comparable in nutrient balance by regulating to a similar intake target.

METHODS

Nutritional geometry and the right-angled mixture triangle

Nutritional geometry (Raubenheimer 2011, Simpson and Raubenheimer 2012) is a state-space modeling approach used to investigate how an animal responds to the challenge of balancing multiple variable nutrient requirements in a dynamic, nutritionally multidimensional environment. This approach has been used successfully to disentangle the relationship between nutrient balance and diet regulation across diverse taxa, both in captive experiments and in observations of free-ranging wild animals (Simpson and Raubenheimer 2012, Nie et al. 2014).

Two central concepts of nutritional geometry are: (1) the current nutritional state of an animal; and (2) its intake target, which is the animal's optimal nutritional state and the state toward which the feeding regulatory systems are predicted to

aim. In order for an animal to reach its intake target, it needs to either consume a single food that is optimally balanced with respect to nutrients, or in the absence of an optimally balanced food an animal can reach its intake target by mixing its diet between imbalanced yet complementary foods. If an animal is restricted to imbalanced and/or noncomplementary foods, it is forced to make behavioral rules of compromise, a concept which is beyond the scope of this study yet has been discussed in detail elsewhere (Raubenheimer and Simpson 1997, Simpson and Raubenheimer 2012).

While many insights into nutrient regulation have been derived from laboratory studies incorporating amounts-based nutritional geometry, obtaining accurate measures of amounts can be difficult in field-based research. For this reason, nutritional data from studies is often measured as a proportion or percentage, for example, studies investigating the food habits of wild bears often use scat-based data to estimate the proportions of different types of foods in the diet (López-Alfaro et al. 2015). This is not necessarily a liability, because proportion-based measures can in many circumstances be germane to addressing certain nutritional questions than are amounts-based measures (Raubenheimer et al. 2014b).

The RMT is a variant of nutritional geometry specifically designed for modeling mixtures expressed as percentages or proportions, for example, individual foods (mixtures of nutrients), observed diets (mixtures of foods and their constituent nutrients), or optimal diets. In an RMT model, each mixture (e.g., food or diet) is plotted as a Cartesian point within an *n*-dimensional *nutrient space*, the position of which is determined by its three-dimensional (e.g., protein:fat:carbohydrate) composition. In Fig. 1, we show a three-dimensional RMT, with carbohydrate and lipid represented on the *x*- and *y*-axes (the explicit axes), respectively. Protein is represented on the implicit *z*-axis, where the value of the *z*-axis varies inversely with distance from the plot origin (i.e., $x = 0, y = 0$). The value of a point on the *z*-axis is the same for any point along a diagonal line of slope -1 which intersects the *x*- and *y*-axes at the same relative value (e.g., 20% on the *x*-axis and 20% on the *y*-axis). As the value of points in the mixture triangle must sum to 100%, the value of

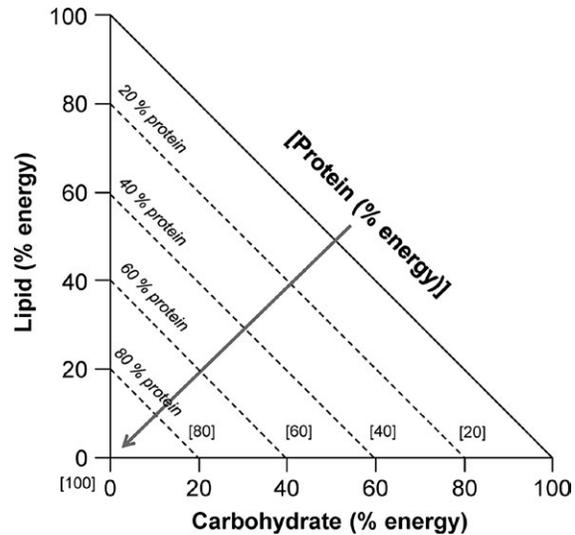


Fig. 1. Right-angled mixture triangle in three nutrient dimensions (protein, lipid, and carbohydrate) expressed on a % energy basis. Protein is represented on the implicit axis, and increases in value as it approaches the plot origin (shown by the arrow). Dashed lines with a slope of -1 indicating constant percentages of protein for different combinations of carbohydrate and lipid are given.

a point on the implicit *z*-axis is equal to $100 - (\text{the value of } x) - (\text{the value of } y)$.

In Fig. 2, we plotted the macronutrient composition of the self-selected diets of captive bears (Erlenbach et al. 2014). The primary (1°) intake target is plotted as an oval indicating the region of nutrient space occupied by diets self-selected by bears provided with food combinations that enabled them to independently regulate their intake of access to protein, lipid, and carbohydrate independently. Results showed that the bears selected a diet in which 17% of energy was contributed by protein, and the bulk of the remaining 83% by fat. Bears selected the same ratio of protein to nonprotein between spring (black triangle) and fall (large black circle) treatments, although bears preferred higher lipid intake in the latter season. Bears offered different combinations of foods which enabled them to regulate protein and fat independently, but not carbohydrate (which was absent from the diet), also selected a diet with 17% protein, in this case using fat to make up the 83% of nonprotein energy (small black circle). Similarly, when able to

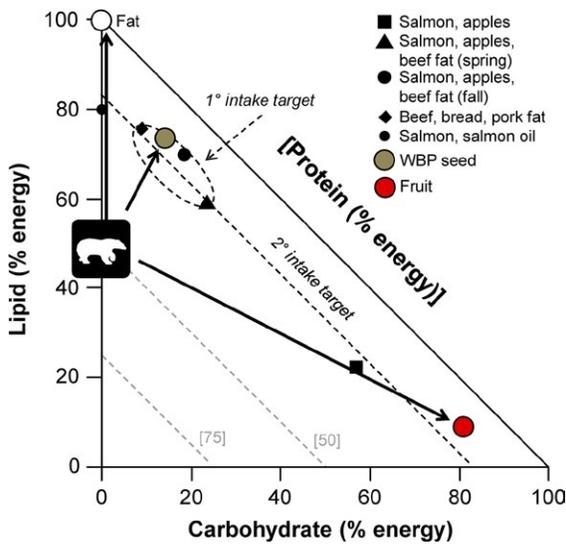


Fig. 2. Right-angled mixture triangle depicting a graphical representation of a hypothetical bear. The diets self-selected by captive bears (Erlenbach et al. 2014) are shown as solid black symbols. The 1° intake target is plotted as a dashed oval indicating the general nutrient space of diets self-selected by bears with access to protein, lipid, and carbohydrate. The secondary 2° intake target was plotted as a negatively sloped line in which bears interchangeably utilized carbohydrate and lipid to maintain a 17% protein to 83% nonprotein energy balance. In this example, a grizzly bear has consumed an ungulate (e.g., moose, elk, or deer), and in terms of macronutrient balance is at a current nutritional state of ~50% protein to ~50% lipid energy. We also plotted two important hyperphagia-season foods of grizzly bears, whitebark pine (WBP) seeds and fruit, as well as 100% animal fat (white circle). As the current nutritional state of the bear is much higher in protein balance than optimal (i.e., the intake target), we would predict that the grizzly bear would have strong regulatory priorities to feed on animal fat, WBP seeds, and/or fruit as they are high in nonprotein energy and would allow the bear to reach either intake target.

regulate protein and carbohydrate intake but not fat, which was present in the foods only in low levels, the selected diet was composed of 17% protein with the bulk of the remaining energy coming from carbohydrate (black square). These experiments suggest that the bears have a hierarchy of macronutrient priorities, in which the primary target has a composition of 17% protein,

with the majority of nonprotein energy coming from fat, and when constrained from reaching this three-dimensional intake target they prioritize a two-dimensional target of 17% protein in which the remaining 83% of energy is derived interchangeably from fat and carbohydrate, depending on what is available. This secondary (i.e., two-dimensional) target (2°) is represented in Fig. 2 by the 17% protein energy isoline.

Foods that lie within the 1° target region or along the 2° target line would be optimally balanced in their ratio of protein to nonprotein energy; conversely, the further food points lay in nutrient space relative to these targets, the more imbalanced they are with respect to the macronutrient regulatory priorities of the animal (Fig. 2). Imbalanced foods that can be combined to reach the primary target region or the intake target line, however, would be complementary, because they allow bears to optimize their macronutrient intake by mixing their diet from foods that are individually imbalanced. We predict that balanced foods, or foods that are complementary with respect to the intake targets of bears, are particularly likely to be involved in bear-human conflict.

In Fig. 2, we also present a hypothetical example where a grizzly bear has consumed an ungulate (e.g., moose [*Alces alces*], elk [*Cervus canadensis*], or deer [*Odocoileus* spp.]), and in terms of macronutrient balance is at a current nutritional state of ~50% protein to 50% lipid energy. We also plotted the macronutrient ratios of two wild foods, fruit and whitebark pine (WBP) seeds, based on Coogan et al. (2014) and Lanner and Gilbert (1994), respectively. The macronutrient content of foods was expressed as a percentage of metabolizable energy using Atwater factors (Merrill and Watt 1973) following Coogan et al. (2014). Here, WBP seeds composed of ~73% lipid and 14% carbohydrate would have a protein content of 13%, and fruit would have an approximate percent protein:fat:carbohydrate ratio of 10:10:80 (Fig. 2). Because the animal's current nutritional state in Fig. 2 is proportionally much higher in protein energy than the intake target, we would predict that the grizzly bear would be highly motivated to feed on complementary foods high in nonprotein energy which would allow it to reach either the 1° or 2° intake target. Given their positions in the RMT, we would predict that the

bears would most highly prioritize the intake of WBP seed, which would take it to the 1° intake target, or otherwise target fruit to reach the 17% protein 2° target, albeit at a point higher in carbohydrate than the 1° target. We also included a food point for 100% animal fat, to demonstrate that bears can also reach the 2° intake target by feeding along the lipid axis; however, such a situation may be unlikely to occur in the wild (Coogan et al. 2014), except, for example, through whale blubber scavenging in coastal regions. The proximity of WBP seeds to the 1° intake target suggests that they are a close to optimally balanced and a highly desirable food item. While we have empirical evidence that fruit and WBP seed are important foods for grizzly bears, we could theoretically predict *a priori* that food occupying the same regions of nutrient space would have a similar appeal and function.

Nutritional data for anthropogenic foods

To examine the relationship between anthropogenic foods and grizzly bear–human conflict, we obtained macronutrient estimates for a variety of anthropogenic foods eaten by North American grizzly bears, including examples from agricultural sources, bird and pet foods, and human foods (Appendix Table A1). Foods from agricultural sources included honey (apiaries), fruit (orchards), and grains. Pet foods included estimates for both cat and dog foods; however, despite the wide variety of dog and cat foods, most manufacturers do not provide carbohydrate or ash estimates of feed and for this reason we present a limited assortment. In order to model human foods available to bears, we obtained macronutrient estimates of foods commonly consumed by hikers, campers, and other outdoor enthusiasts. As we know of no data illustrating bear selection of campsite foods, human foods modeled are examples only, and were not meant to be exhaustive for obvious reasons. Macronutrient data were obtained from the USDA National Nutrient Database (U. S. Department of Agriculture, Agricultural Research Service 2013), Feedipedia Animal Feed Resources Information System (INRA 2013), and manufacturers' information (dog and cat foods). Macronutrient estimates were converted to percent metabolizable energy following Coogan et al. (2014). We note that

nutritional analysis methods may differ, and nutritional compositions of modeled foods may differ from those available to bears; however, we collected nutritional data from the USDA and Feedipedia databases because they provide a comprehensive inventory of food items and allowed us to “standardize” our nutritional data collection to minimize possible between-study heterogeneity in nutritional analysis methods and estimates.

Modeling scenarios

We explored the relationship between bear–human conflict and the macronutrient balance of anthropogenic foods in three RMTs. In our first, we demonstrated how bear foraging behavior aimed at optimizing macronutrient intake may be confounded with energy maximization in energy-based studies. We first plotted individual anthropogenic foods within the RMT based on their macronutrient compositions, after which we categorized foods based on their relative metabolizable energy content (kcal/g dry matter). Foods were categorized as being relatively high energy (≥ 5.25 kcal/g dry weight), medium energy (>4.00 – 5.25 kcal/g), or low energy (≤ 4.00 kcal/g) using arbitrary cut-off points. Equivalent categorizations are often used in ecological studies as synonymous with food “quality” (e.g., Spitz et al. 2010).

In our second example, we examined the relationship between the macronutrient balance of anthropogenic foods, optimal macronutrient requirements, and the region of nutrient space available to wild bears. Within an RMT, points representing all of the foods available to an animal can be connected to create a polygon defining the area of the nutrient space that is “accessible” to that animal—i.e., the region within which the point representing diet composition is constrained to fall. Here, we used data from Coogan et al. (2014) to plot the estimated nutrient space available to grizzly bears in Alberta, Canada, during the late-fall hyperphagic period to examine the relationship between wild and anthropogenic foods. The nutrient space indicated the range of protein to nonprotein energy ratios potentially achievable by bears mixing their diet among available wild foods. The nutrient space was divided into two sections indicating the estimated nutrient space when fruit is plentiful

enough for bears to effectively mix their diet (dark gray and light gray sections of nutrient space combined) and during a fruit crop failure (dark gray section of nutrient space only). Overlap between the nutrient space polygon and the intake target line would suggest that bears are able to consume an optimally balanced diet by consuming complementary resources.

Although we modeled only a very small selection of human foods in the above scenarios, the range we modeled is to some extent representative given the high preponderance of fat and, particularly, carbohydrate in modern human food (Popkin et al. 2012, Raubenheimer et al. 2014a). In our third scenario, we examine this in the North American context, and interrelate it to our model of bear macronutrient selection, by exploring the frequency of different macronutrient ratios in the 7613 macronutrient-containing foods from the USDA foods database. Data were represented as a contour plot within the RMT, color-coded to show the logarithm of the frequency of foods appearing in each 2.5% × 2.5% lipid × carbohydrate cell, where dark red represents the highest frequency and dark blue the lowest frequency. Furthermore, it follows that food attractants of bears containing anthropogenic meats (e.g., garbage and camping foods) would also have higher lipid contents than available wild game. For comparison, we plotted the % energy composition of some common domestic cuts of beef, pork, and lamb (including separable fat plus lean, as well as lean only) and game-derived meat (including small mammals) in the USDA database.

RESULTS

Our first example demonstrates that the energy density of foods generally increases as the proportion of energy contributed by lipid increases (Fig. 3). High-carbohydrate foods, by contrast, generally had the lowest energy density. Some high-energy, high-lipid foods were in close proximity to the 1° intake target. Foods from each energy-density category (high, medium, and low), however, had protein: non-protein energy ratios in proximity to the 2° intake target. Among agricultural foods, honey, fruit, and grain were very high in carbohydrate content. Of bird feed, seeds were close to optimally balanced in protein to nonprotein energy,

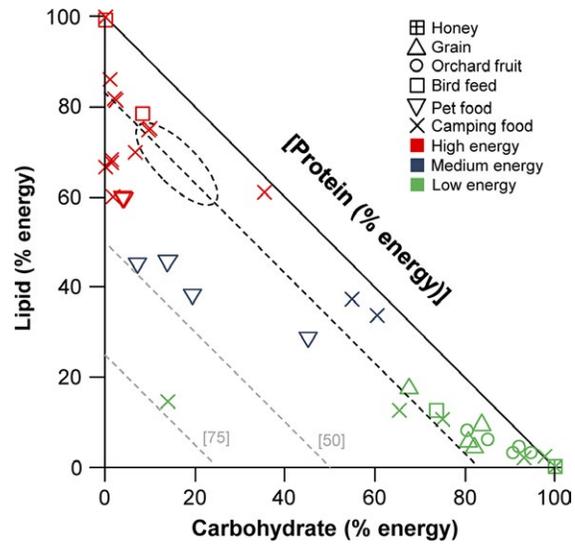


Fig. 3. Right-angled mixture triangle depicting the estimated macronutrient content of anthropogenic foods potentially consumed by grizzly bears in North America, given as a percentage of metabolizable energy. Foods were classified by their relative metabolizable energy content (kcal/g dry matter): high energy (≥5.25 kcal/g dry weight; red symbols), medium energy (>4.00–5.25 kcal/g; blue symbols), and low energy (≤4.00 kcal/g; green symbols).

whether relatively higher in carbohydrate or lipid, while suet was composed solely of lipid energy. Pet food (dog and cat) was generally high in protein relative to the intake target.

Our second RMT analysis of anthropogenic foods shows that in many cases their nonprotein energy content was higher than natural foods available to wild bears (as shown by the nutrient space polygon) in Alberta (Fig. 4). Note that in this ecosystem, bears are unlikely to reach the 1° intake target by consuming natural foods; however, they can reach the 2° intake target when wild fruit is available. A number of human foods were high in carbohydrate or lipid relative to the intake target and to the nutrient space accessible to wild Alberta bears. The nutrient space polygons indicate that bears are unable to optimize their macronutrient intake in late-fall if fruit is unavailable (i.e., only the light gray nutrient space polygon falls on the intake target line; Coogan et al. 2014, Fig. 4). In the absence of fruit, however, a number of anthropogenic foods can be substituted as sources of nonprotein energy in

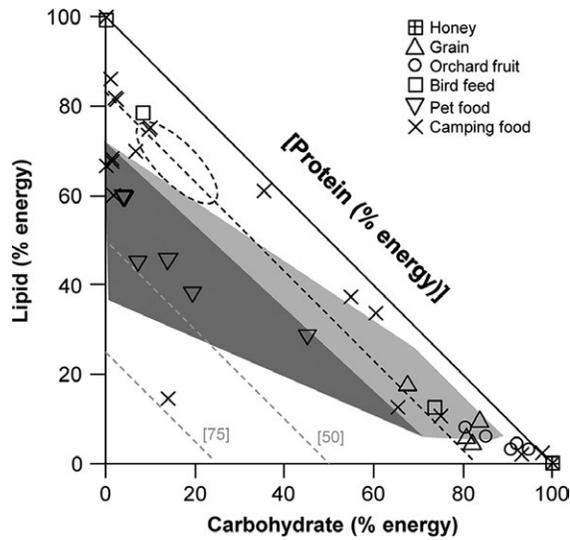


Fig. 4. Right-angled mixture triangle showing the estimated macronutrient content of anthropogenic foods potentially consumed by grizzly bears in North America (% metabolizable energy) including gray-shaded polygons representing the estimated nutrient space of wild foods available to grizzly bears in Alberta, Canada, during the late-fall hyperphagic period (Coogan et al. 2014). The dark gray and light gray polygons combined indicate the nutrient space when fruit is plentiful, while the dark gray polygon indicates the nutrient space in the absence of fruit (i.e., a fruit crop failure). Overlap between the nutrient space polygon and the intake target indicates that bears may be able to optimize their macronutrient balance by mixing their diet between available wild foods, while lack of overlap indicates that bears are unlikely to optimize their diet by consuming available natural foods.

order to optimize macronutrient intake, including orchard fruit, honey, bird feed, grain, and a number of human foods. Therefore, we would expect increased grizzly bear-human conflict associated with these anthropogenic foods when fruit crops fail.

The frequency of macronutrient ratios in North American foods shows a high preponderance with very high proportional carbohydrate content, a second ridge at low carbohydrate and relatively high fat content (40–80%) and a dark blue trough in the region representing high protein (near the origin; Fig. 5). Anthropogenic foods are, therefore, more likely to provide

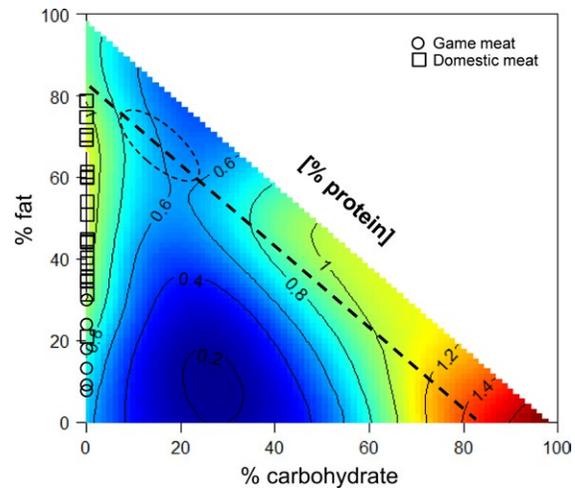


Fig. 5. RMT showing the frequency of different macronutrient ratios in the 7613 macronutrient-containing foods from the USDA foods database. The data are represented as a contour plot, color-coded to show the logarithm of the frequency of foods appearing in each 2.5% x 2.5% lipid x carbohydrate cell, where dark red represents the highest frequency and dark blue the lowest frequency. For comparison, we plotted the macronutrient composition (% metabolizable energy) of some common domestic cuts of beef, pork, and lamb, vs. game-derived meat (including small mammals).

bears with carbohydrate-rich, and to a lesser extent lipid-rich, foods than high-protein foods. Interestingly, there is a low frequency of foods in the 1° intake target region; anthropogenic foods are more likely to allow bears to reach the 2° intake target. Thus, high-carbohydrate anthropogenic foods are more likely to be sources of grizzly bear-human conflict. The green/yellow ridge corresponding with low carbohydrate and high fat (40–80% of macronutrient energy) represents largely meats derived from livestock. Data points representing the composition of wild game (7–29% lipid energy) were below the high-fat ridge of anthropogenic meats, while points representing domestic cuts were generally higher in lipid (32–78%). Only 97% lean ground beef (22% lipid energy), a heavily mechanically processed product, was found among the nutritional estimates for wild game meat, while some leaner trimmed cuts were just above the high range of lipid in game meat.

The higher lipid content of domestic meats may make them more attractive to grizzly bears than lean wild meats, making them a potential source of conflict.

DISCUSSION

Here, we used nutritional geometry and the concept of behavioral regulation of macronutrient intake to further understand why certain foods are particularly attractive to bears and likely to cause management issues. This macronutrient-focused approach gives rise to fundamentally different predictions than the conventional food and energy-focused approaches. Specifically, the models predict that conflict is likely when the availability of high-lipid and high-carbohydrate natural food sources does not allow bears to meet their nutrient intake targets but anthropogenic foods do allow bears to satisfy these preferences. It is clear that under these circumstances anthropogenic foods can offer grizzly bears sources of nonprotein energy, especially carbohydrates, which likely exacerbates food-related grizzly bear-human conflict due to nutrient-specific foraging behavior. Such foods, therefore, are likely to be sources of conflict. While protein may be limiting to bears in an absolute sense (amount), nonprotein energy sources are generally rarer and less seasonally available, and natural bear diets are likely to be high in protein relative to nonprotein macronutrients. Because the intake targets were derived from hyperphagic and nonhyperphagic periods, these models likely apply to grizzly bear foraging throughout the active season. Prior to the hyperphagic season, grizzly bears often consume large amounts of vegetation some of which is close to the intake target in nutrient balance, albeit higher in protein (Coogan et al. 2014); however, green vegetation is consumed far less by grizzly bears during hyperphagia because it tends to become less palatable. Therefore, if the availability of soft or hard mast (or other natural foods high in nonprotein energy) during the hyperphagic period is insufficient to satisfy grizzly bear preferences they are likely to experience a greater nutrient imbalance than during prehyperphagia, especially if starchy roots are also limiting.

Furthermore, it is possible that grizzly bears may be less tolerant of nutritional imbalances during the critical prehibernation hyperphagic season, resulting in an increased drive to obtain limiting nutrients. Another factor contributing to increased incidences of grizzly bear-human conflict observed during hyperphagia may likely be because bears require greater absolute amounts of food during this time; however, RMT models based on proportional data do not address this.

The relationship between the proportional lipid content of foods and their metabolizable energy content suggests that classification based on energy alone confounds feeding behavior aimed at optimizing macronutrient intake. While the high-lipid 1° intake target lies within the high-energy nutrient space, a purely energy-based foraging paradigm (energy maximization) would miss the fact that high-carbohydrate yet low energy-density foods (e.g., honey, fruit, and grain) offer bears sources of nonprotein energy that may allow them to optimize macronutrient intake by reaching the 2° intake target. Aside from the energy density of foods increasing as the proportion of the higher energy macronutrient (lipid) increases, the energy density of foods also increases as the overall concentration of macronutrients increases (Raubenheimer 2011). Fruit, for example, has relatively low energy density due to high fiber and water content which dilutes macronutrient concentration, and bears are constrained by foraging intake rates when consuming macronutrient-dilute foods such as fruit (Welch et al. 1997). Nonetheless, bears target fruits when available, most likely because they provide a source of otherwise limiting nonprotein energy to balance their macronutrient intake.

Bears often eat garbage, which was not explicitly examined in this study. Although difficult to model a nutrient space for garbage, it has the potential to encompass a wide range of macronutrient values. For example, a nutrient space for campground garbage in our RMT analysis could be estimated by forming a nutrient space polygon around macronutrient estimates for camping food. Another approach to estimating the composition of garbage would be to use the macronutrient frequencies of anthropogenic foods in Fig. 5. As human discards are likely to be relatively low in protein due to the relatively higher cost

of this macronutrient compared with fats and carbohydrate (Brooks et al. 2010), the macronutrient balance of edible garbage is more likely to lie in the high-frequency high-carbohydrate and -fat regions of Fig. 5. The macronutrient composition of garbage, therefore, is very likely to provide problem bears with sources of nonprotein energy, particularly carbohydrate, with much of it relatively well balanced relative to their intake target (Fig. 5). It is not surprising then that access to large amounts of garbage has resulted in bear populations with high densities, large body sizes, short foraging periods, and reduced denning periods (Craighead et al. 1995, Beckman and Berger 2003, Baldwin and Bender 2010); such bears are likely to take in a large amount of food energy with a greater probability of it being optimally balanced in macronutrient content, subsequently optimizing mass gain.

Furthermore, any meat that is found in garbage is more likely to be higher in lipid than wild game. It has been well documented that meat from domestic livestock are typically higher in lipid than wild animals (Mann 2000, Hoffman and Wiklund 2006, Kuipers et al. 2010). For example, the fat content of store-bought red meat reported in an Australian study (which we assume are similar to North American meats) ranged from 17 to 26 g/100 g (fresh weight) for store-bought lamb and 5–19 g/100 g for beef, with the possibility of fat-trimmed cuts being lower than 5% (Mann 2000 and references therein); however, the fat content of most wild game has been reported to be <3% for several species (Cordain et al. 2002, Hoffman and Wiklund 2006 and references therein), including those consumed by grizzly bears (e.g., elk and deer), and <2% for small mammals (Cordain et al. 2000). Even extra-lean ground beef has a much higher fat content than many wild meats (Texas Parks and Wildlife 2015). While it may be tempting to infer from this that domestic livestock available to grizzly bears are higher in lipid content than wild ungulates, which may, therefore, increase their attractiveness as prey, the muscle tissue of free-ranging beef (as opposed to feed lot-fed beef) has been reported as being only slightly higher or similar to the fat content of elk and deer (Cordain et al. 2002). Other species, however, such as sheep, tend to be higher in fat content than beef (Mann 2000) and are often

predated by grizzly bears (Gunther et al. 2004). Additionally, free-ranging livestock receiving a steady supplemental food supply are likely to have higher lipid content than wild game during years of low ecosystem productivity. Other factors, such as ease of locating and capturing prey, may be influencing livestock depredation. The relationships between macronutrient content of available wild game and patterns of livestock depredation by grizzly bears, therefore, requires more research to resolve.

Consideration of macronutrient balance has implications for grizzly bear management, because in order for a particular management strategy to be effective, an understanding of an animal's nutritional requirements, the habitat's ability to satisfy these requirements, and the animal's responses to nutritional constraints are required. For example, bears may forage in "attractive sinks" (Nielsen et al. 2006), because foods available in these locations may have favorable or complementary nutrient balances (Coogan et al. 2014). Furthermore, the concept of macronutrient balance helps us to understand why bears are attracted to areas to feed on other high-carbohydrate yet energy-dilute foods such as grains, for example, near railway tracks (Huber et al. 1998, Waller and Servheen 2005, Dorsey 2011)—we would predict that such a situation would be especially appealing for bears also feeding on train-killed ungulates. Our analysis suggests that anthropogenic foods which allow bears to reach their intake target, in particular high-carbohydrate foods which allow them to reach their 2° intake target, could be further identified as potential flashpoints of conflict and be targeted for management. A macronutrient-focused approach is also relevant to supplemental feeding programs; however, we recognize that such programs are often controversial (Herrero et al. 2005, Elfström et al. 2014a, Steyaert et al. 2014).

The role of nutritional ecology in the conservation of bears has global relevance. For example, the most widely distributed of all bears, *U. arctos*, is found across the northern hemisphere in North America, Asia, and Europe (Bojarska and Selva 2011). Grizzly bears, American black bears (*Ursus americanus*), and giant panda (*Ailuropoda melanoleuca*) have very similar digestive efficiencies (Pritchard

and Robbins 1990), and the polar bear (*Ursus maritimus*) is likely similar to grizzly bears in preferring a high-lipid to protein diet (Erlénbach et al. 2014). In the face of climate change, more explicit knowledge of the macronutrient preferences of polar bears is necessary to understand the impact of a changing food supply, such as their ability to survive on terrestrial foods (Dyck and Kebreab 2009, Rode et al. 2010). In addition, macronutrient regulation is likely to play a role in food-related human-wildlife conflict of other bears, including the American black bear (Baruch-Mordo et al. 2008), sloth bear (*Melursus ursinus*; Rajpurohit and Krausman 2000), sun bear (*Helarctos malayanus*; Fredriksson 2005), spectacled bear (*Tremarctos ornatus*; Goldstein et al. 2006), and Asiatic black bear (*Ursus thibetanus*; Oka et al. 2004).

An important topic of future research is to investigate the dynamics of bear macronutrient intake targets both between and within species. For example, how might the macronutrient intake target of bears differ between sex and age classes throughout the active season, and are such differences, if any, related to the demographic of bears more likely to be involved in food-related conflict? Another important question to address is how might the intake targets of captive bears differ from those in the wild, or among those in different habitats (i.e., experiencing different environmental conditions). For example, the observation that European brown bears in anthropogenic environments seem to have diets similar in quality as their wild counterparts (Elfström et al. 2014b) would be expected if they regulated their nutrient intake toward a similar target. This has been suggested as a mechanism behind the foraging behavior of the European badger (*Meles meles*; Kohl et al. 2015), an omnivorous carnivore populations of which maintain a similar nutrient intake despite residing in different habitats (Remonti et al. 2011). It is possible, however, that some populations of bears may show local environmental adaptations (Shafer et al. 2014) that may affect their macronutrient preferences.

In overview, we have presented a framework for developing a more refined and predictive approach to considering wildlife foraging behavior

in a conservation and management context that can be applied broadly across taxa. Given the widespread nature of macronutrient regulation among functional groups and taxa (Simpson and Raubenheimer 2012), nutritional ecology and geometric analysis offers an especially useful framework for investigating food-related human-wildlife conflict more generally. Such studies can be extended to include the constituents of macronutrients (e.g., amino and fatty acids) and other nutritional variables of interest. For example, Nie et al. (2014) demonstrated the role of the micronutrients calcium and phosphorus in the migration patterns and reproductive cycles of wild giant pandas. Obligate carnivores, which recent evidence suggests also regulate their intake of macronutrients (reviewed in Kohl et al. 2015), may find domestic animals more appealing prey if they have higher lipid contents than wild game. This might explain why high rates of livestock depredation by wolves (*Canis lupus*) can occur despite the availability of large populations of wild prey (Patalano and Lovari 1993), and is especially relevant given that lipid may also be an increasingly limiting resource as trophic level increases (Wilder et al. 2013). Yet, information regarding the basic nutritional requirements of wild animals, and the ability of habitats to provide for these requirements, are often limiting when considering nutritional aspects of conservation. Essential nutritional studies of problem wildlife, as well as threatened and endangered species, are necessary to provide the basis of a nutritional framework for wildlife conservation.

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