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Macronutrient optimization and energy maximization determine diets of brown bears

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Many animals consume mixed diets that maximize their fitness by optimizing macronutrient intake. We tested whether brown bears (*Ursus arctos*), generalist omnivores that hibernate, regulated their diet to a common nutrient target, achieved a nutrient target related to fitness, and selected a nutrient target that differed between seasons and from other species with differing life histories. When given unlimited access to 2 or 3 highly digestible foods containing primarily protein, carbohydrate, or lipid, brown bears selected mixed diets in which protein provided 17% ± 4% *SD* of the metabolizable energy and 22% ± 6% of the dry matter. This dietary protein content maximized the rate of gain per unit of energy consumed, is similar to the level preferred by other omnivores, and is less than that preferred by obligate carnivores. Between seasons, bears selected similar dietary protein levels, although the proportion of lipid was higher during the fall than during the spring. Bears strongly preferred lipids over carbohydrates, as did other carnivores, but they used lipids and carbohydrates with equal efficiency to produce a dietary protein content that maximized mass gain per unit of energy intake. Thus, dietary sources of lipids and carbohydrates play an interchangeable and important role in determining the productivity of bears that goes beyond their role in providing energy.

Key words: brown bear, carbohydrate, diet, fat, foraging, geometric framework, protein

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Energy acquisition has been the predominant focus of foraging ecology research since the field was first conceptualized in the 1960s (MacArthur and Pianka 1966). However, foraging effort and diet selection are not purely functions of energy acquisition (Simpson and Raubenheimer 2012). Whenever possible, animals also must select an appropriate mixture of macronutrients (i.e., protein, carbohydrates, and lipids). Macronutrient optimization can have significant effects on growth, immune responses, longevity, and fecundity (Simpson et al. 2004; Robbins et al. 2007; Simpson and Raubenheimer 2009; Cotter et al. 2011). Therefore, it is likely that both energy and macronutrient goals, as well as selection opportunities, shape the foraging behaviors of wild animals.

Foraging decisions made by many animals, such as primates, rodents, and carnivores, are partially based on meeting macronutrient goals (Robbins et al. 2007; Sørensen et al. 2008; Felton et al. 2009; Mayntz et al. 2009; Hewson-Hughes et al. 2011, 2013). For example, free-ranging brown bears (*Ursus arctos*) have been observed to leave energetically more valuable salmon resources to consume fruits, even though energy maximization theory predicts that bears should choose to consume salmon only (Rode et al. 2006; Fortin et al. 2007). Subsequent feeding studies with captive brown bears showed that mixing high-carbohydrate fruit and high-protein salmon maximized mass gain per unit of energy intake by optimizing dietary protein content. Thus, intrinsic nutritional characteristics of foods as well as their gustatory or olfactory appeal may

TABLE 1.—Macronutrient compositions of foods offered to brown bears (*Ursus arctos*) to determine their preference for protein, fat, and carbohydrates.

		% of dry matter			% of metabolizable energy[a]			
Diet items	Dry matter (%)	Protein	Carbohydrate[d]	Lipid	Protein	Carbohydrate	Lipid	Digestible energy[b] (kcal/g DM[c])
Salmon	29	67	< 1	19	62	< 1	38	5.2
Beef	30	66	< 1	27	54	< 1	46	5.9
Apples	15	3	68	5	3	82	15	2.8
Bread	69	16	70	3	18	76	6	3.9
Salmon oil	100	0	0	100	0	0	100	9.1
Beef fat	89	3	< 1	96	1	< 1	99	9.1
Pork fat	80	3	< 1	96	2	< 1	98	9.1

[a] Metabolizable energy calculated using Atwater specific factors for meat protein (4.27 kcal/g), fruit protein (3.36 kcal/g), grain protein (4.05 kcal/g), fruit digestible carbohydrate (4.00 kcal/g), grain digestible carbohydrate (4.20 kcal/g), meat lipid (9.03 kcal/g), fruit lipid (8.37 kcal/g), and grain lipid (8.37 kcal/g—Merrill and Watt 1973).

[b] Digestible energy coefficients from either published values (Pritchard and Robbins 1990; Welch et al. 1997; Hilderbrand et al. 1999; Rode and Robbins 2000) or calculated using the equation in figure 2 from Pritchard and Robbins (1990).

[c] DM = dry matter.

[d] Digestible carbohydrate as a percent of the dry matter calculated as 100 − (protein + fat + total digestible fiber + ash).

guide dietary mixing in bears (Rode and Robbins 2000; Robbins et al. 2007).

Although previous research has explained many facets of diet selection by bears, our understanding is still incomplete. To date, captive feeding studies have largely focused on protein and carbohydrate selection and metabolism (Welch et al. 1997; Hilderbrand et al. 1999; Rode and Robbins 2000; Felicetti et al. 2003; Robbins et al. 2007). However, most bears, including brown bears, polar bears (*U. maritimus*), Asiatic black bears (*U. thibetanus*), sloth bears (*Melursus ursinus*), and sun bears (*Helarctos malayanus*) have the opportunity to consume high-lipid foods (e.g., nuts, some tropical fruits, marine mammals, eggs, and reproducing insects [(Stirling and McEwan 1975; Mattson et al. 1992; Joshi et al. 1997; Gende et al. 2004; Steinmetz et al. 2013]). To ignore the importance of lipids in diet selection belies the complementary and interacting nature of macronutrients, oversimplifies the choices bears experience in the wild, and offers a potentially biased and incomplete understanding of diet selection. A more complete understanding of the nutritional needs and dietary goals of bears will allow us to identify important foods, understand motivations for bear foraging behavior, understand how macronutrient and energy intake can influence individual success and population trends, and explain evolutionary and life-history relationships between bears and other species.

Our goal was to expand on current understanding of bear diet selection using macronutrient analysis of food choices by bears independent of food availability, foraging efficiency, ecological risk, and other competing needs that exist in the wild. The study of macronutrient balancing has been revolutionized by using the geometric framework proposed by Raubenheimer et al. (2009) in which nutrient targets (i.e., nonrandom combinations of macronutrients that confer a functional advantage over other combinations) can be identified and the multidimensional and dynamic nutritional priorities of animals can be explained. We used the geometric framework as a guide to test whether brown bears regulate their diet to a common nutrient target, achieve a nutrient target that is related to fitness, and select a nutrient target that differs between seasons and among other species with different life histories. We hypothesized that brown bears should select foods that optimized their dietary protein content, maximized their energy intake by selecting fats over carbohydrates, and maximized their efficiency of mass gain. We further hypothesized that fat would be less preferred in the spring than in the fall when bears were focused nutritionally on accumulating large fat reserves for hibernation.

MATERIALS AND METHODS

Animals and facilities.—We used 2 adult males brown bears ($\bar{X}$ = 288 kg, range = 281–295 kg) and 5 adult female brown bears ($\bar{X}$ = 178 kg, range = 150–232 kg) housed at the Washington State University Bear Research, Education, and Conservation Center, Pullman, Washington. Bears were housed in 3 × 3-m indoor dens connected to 3 × 5-m outdoor runs. We weighed all bears with electronic scales to the nearest 0.5 kg at the beginning and end of each feeding trial. The study was conducted in accordance with animal care and use guidelines of the American Society of Mammalogists (Sikes et al. 2011) and was approved by the Washington State University Institutional Animal Care and Use Committee (protocol 04072-003).

Macronutrient regulation.—To assess macronutrient intake and regulation by bears, we provided diets that gave bears access to combinations of 2 or more foods at a time and allowed them to choose between foods that offered primarily protein (chinook salmon [*Oncorhynchus tshawytscha*] or lean beef), carbohydrate (apples [*Malus pumila*] or bread), or fat (beef or pork fat or salmon oil [Jedwards International, Inc., Quincy, Massachusetts]; Table 1). Two food combinations that offered ad libitum protein, carbohydrate, and lipid (salmon, apples, and beef fat; and lean beef, bread, and pork fat) were fed to test for regulation of all 3 macronutrients, as well as to determine if diets were being chosen based on taste, smell, or texture, rather than regulation of macronutrient intake. Selection of the same ratio of macronutrients from the 2 different food combinations would support the contention that

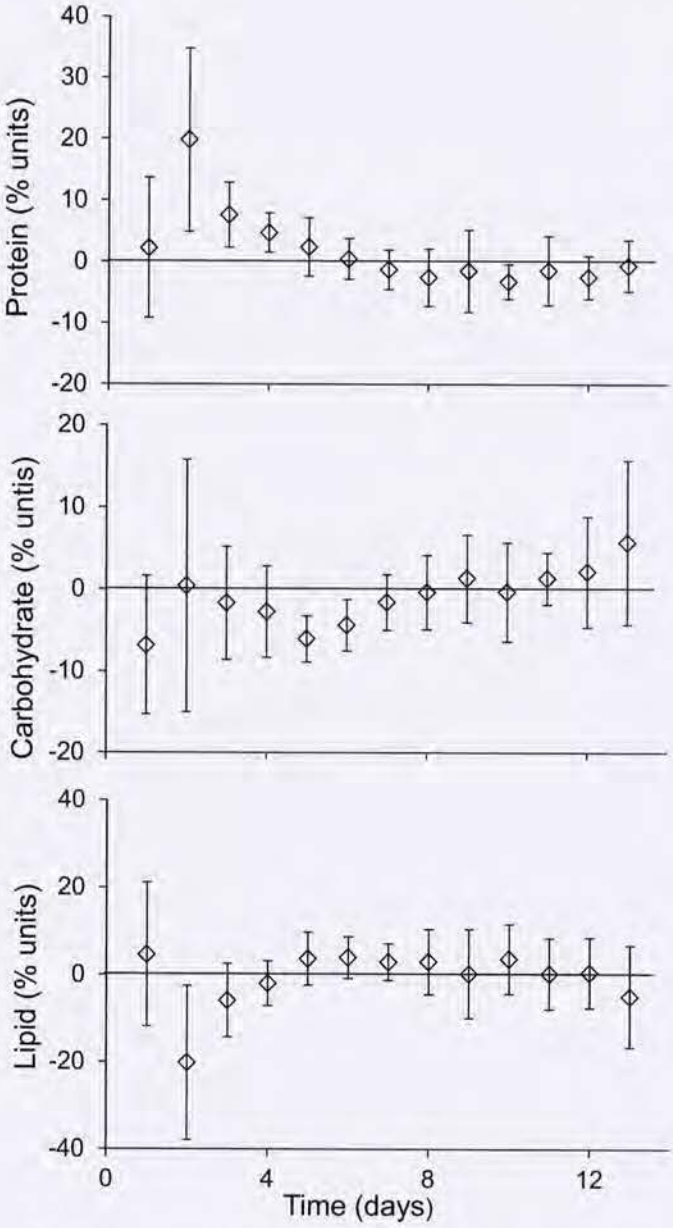

Fig. 1.—Average (± 1 *SD*) daily differences from the mean intake of protein, carbohydrate, and lipid (% of metabolizable energy) for brown bears (*Ursus arctos*) consuming the salmon, apple, and beef fat diet and the lean beef, bread, and pork fat diet. The mean intake for each feeding trial excluded the first 2 days and final day for each bear (see "Materials and Methods").

the selection was a result of macronutrient-specific regulation. We fed the bears salmon, apples, and beef fat during the fall and spring to compare macronutrient goals between seasons. A protein and lipid diet (salmon and salmon oil) also was fed to simulate the diet of a strict carnivore, such as a polar bear, that would not typically consume significant carbohydrates (Hobson et al. 2009). In addition, we used data from a previous ad libitum salmon and apples study (Robbins et al. 2007) to assess protein and carbohydrate mixing.

Bears were familiarized with all test foods as part of their routine feeding program for months to years before beginning any trial. Each feeding trial included 3–5 bears and lasted for 8–19 days or until diet selection stabilized. Fall feeding studies occurred from August to October 2010–2012 and spring studies occurred in April 2012 and 2013. Because of the desire to use nonobese bears that would have appetites typical of most wild bears, we fed bears at restricted levels until they were placed on the ad libitum diets.

All foods were fed ad libitum in either discrete meals or available 24 h/day. Food was weighed before feeding and either offered twice daily because of the difficulty in feeding a liquid lipid (salmon oil) or distributed in 3 separate, randomly ordered piles (1 each of a primary protein, carbohydrate, and lipid source) in each bear's den. Salmon and salmon oil (fed with a laboratory squirt bottle) were offered to bears simultaneously and repeatedly throughout each feeding, allowing bears to choose which item they wanted at any time. Feeding continued until the bear was satiated and walked away. Any remaining salmon or oil was weighed to determine the amount consumed. In other trials, we collected uneaten food after 24 h and weighed and corrected for moisture loss to determine the amount consumed.

Representative food samples were collected daily, frozen, freeze-dried, homogenized, and ground prior to analyses. Gross energy was determined by bomb calorimetry, protein (N × 6.25) by a carbon–nitrogen analyzer, and lipid by ether extract. Dietary fiber that is not digestible in bears was estimated by the Prosky method (Pritchard and Robbins 1990). Finally, digestible carbohydrate content was estimated by difference (i.e., 100 − (protein + fat + fiber + ash)). All analyses were conducted at the Washington State University Wildlife Habitat and Nutrition Lab in Pullman, Washington.

The metabolizable energy content of each bear's selected diet was calculated by multiplying the amount of protein, fat, and digestible carbohydrates consumed daily by the Atwater specific factors for energy content (Merrill and Watt 1973). Average daily macronutrient selection values for bears were calculated excluding the first 2 days and last day of each trial. The first 2 days were excluded because animals were adjusting to the diet during that period (Fig. 1), and the last day was excluded because food was removed in the afternoon to ensure gastrointestinal emptying before weighing the following day.

Fitness relationships.—We used mass gain as a fitness indicator because body mass and fatness are determinants of bear survival through hibernation, female reproductive success, and male dominance (Kovach and Powell 2003; Robbins et al. 2012a). Because all bears used in this study were adults, changes in mass should largely reflect changes in fat mass. Following Robbins et al. (2007), regressions were developed between mass gain (g $kg^{-0.75}$ day^{-1}) and digestible energy intake (kcal $kg^{-0.75}$ day^{-1}) for all diets fed during this study. The regressions included the mixed diets in which macronutrient selection was measured, but also included 4 additional salmon and salmon oil diets (protein content ranging from 7% to 60% of dry matter) that were fed to complement previous bear growth studies which largely used protein- and carbohydrate-based diets. The net efficiency of gain (i.e., the

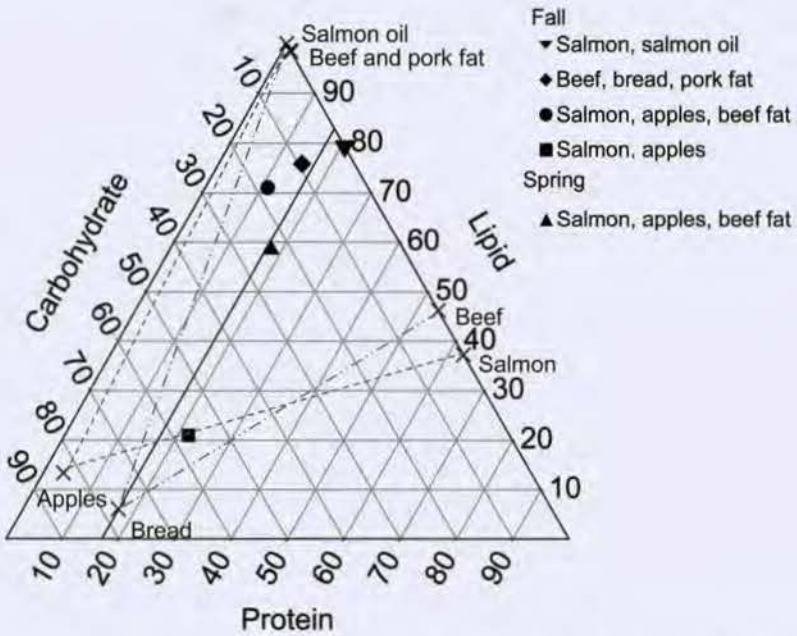

Fig. 2.—Average daily macronutrient selection values (% of metabolizable energy) during ad libitum feeding trials of captive brown bears (*Ursus arctos*) given access to diets of salmon and apples ($n = 4$); salmon, apples, and beef fat ($n = 4$); beef, bread, and pork fat ($n = 3$); and salmon and salmon oil ($n = 5$) depicted in an equilateral mixing triangle. Individual food items are shown as an x, and the area inside the triangle connecting 3 food items (dashed lines) shows the available nutrient-space that bears could have used in selecting their diet. Each axis of the equilateral mixture triangle represents the percent of metabolizable energy from that macronutrient in the diet, which can range from 0% to 100%. The values for each macronutrient extend in the direction that the numbers are slanted. For example, the lipid values run horizontally, carbohydrate values slant downward to the right, and protein values slant upward to the right. The dietary mixture chosen by bears is composed of fractions of energy from each macronutrient that sum to 100%. Therefore, the points shown in the figure, representing bear diet choice, lie at the intersection of the percent contribution of protein, carbohydrates, and lipids to the diet. A reference protein value of 17%, the average level selected by the bears (solid line), is plotted on the graph.

slopes of the regressions) and the maintenance energy cost (i.e., the x-intercepts at zero mass change) estimated from these new and previous regressions were combined to estimate the mixture of macronutrients that maximized the rate of gain per unit of energy intake (Robbins et al. 2007). This allowed us to determine whether the energy source (i.e., carbohydrate versus lipid) affected the rate of gain per unit of energy intake; what concentration of macronutrients, particularly protein, optimized mass gain; and whether bears on ad libitum free-choice feeding trials selected macronutrient ratios at that optimum.

To compare intake to previous studies, maximum intakes from all ad libitum feeding studies were measured. The highest consecutive 3-day intake by each bear was used to calculate their average maximum daily intake (% of body mass and kcal digestible energy/kg). Maximum estimated rates of growth (g $kg^{-0.75}$ day^{-1}) were calculated from the average maximum energy intakes and the regressions describing growth on each diet. To contextualize the energy intake of bears, we compared the bears' average digestible energy intake to the basal metabolic rate of carnivores, $y = 61.9x^{0.77}$, where x is body mass in kg and y is kcal/day (Robbins et al. 2012b).

Statistical analyses.—Linear and curvilinear least-squares regressions were used to model the relationships between intake, growth rate, and dietary protein content. We used analysis of variance and *t*-tests to test for differences between rates of gain, energy intake, percent lipid intake, and seasonal percent intake (PROC GLM and PROC Mixed—SAS Institute Inc. 1998). We used an α level of 0.05 and means are reported $\pm$ 1 *SD*.

Results

Bears did not feed indiscriminately during any feeding trial. They identified the macronutrient target within approximately 3 days of beginning the trials (Fig. 1). However, bears overconsumed lipids and underconsumed carbohydrates during the 1st day. Several bears vomited shortly after consuming large amounts of fat on day 1. This negative feedback presumably led to underconsumption of lipids and overconsumption of protein on day 2. However, the relative proportions of dietary lipids, carbohydrates, and protein did not change from day 3 to day 13 (lipids, $F_{1,108} = 0.86$, $P = 0.42$; carbohydrates, $F_{1,108} = 4.90$, $P = 0.11$; protein, $F_{1,108} = 8.32$, $P = 0.06$).

Bears consistently selected food mixtures in which protein provided 17% $\pm$ 4% of the metabolizable energy and 22% $\pm$ 6% of the dry matter, regardless of the combination of foods offered and the matrix of macronutrient mixtures that was

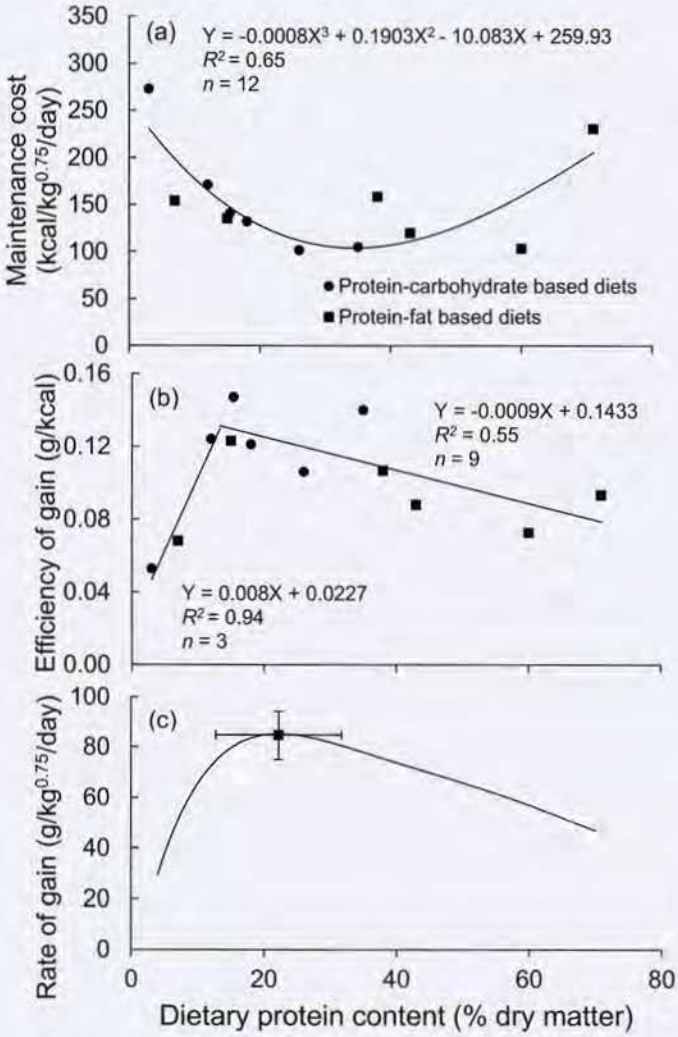

Fig. 3.—a) Brown bear (*Ursus arctos*) digestible energy intake at maintenance, b) net efficiency of gain above maintenance, and c) the rate of gain predicted from the above functions at 800 kcal of digestible energy intake $kg^{-0.75}day^{-1}$ at various dietary protein contents (Robbins et al. 2007; current study). The protein content of diets selected by brown bears (22% ± 6% of the dry matter) when allowed to mix 2 or 3 foods with differing protein, fat, and carbohydrate proportions is shown in C to illustrate that bears selected foods that provided the most efficient dietary protein content for maximizing their mass gain per unit of energy intake.

possible (Fig. 2). Both the maintenance cost (Fig. 3A) and the net efficiency of gain (Fig. 3B) varied in predictable ways with dietary protein content. Both too little and too much protein increased the maintenance cost (Fig. 3A), decreased the net efficiency of gain (Fig. 3B), and thereby decreased the rate of gain per unit of energy intake (Fig. 3C). The dietary protein content that maximized the overall efficiency of gain ranged from ~19% to 25% of dry matter when consuming highly digestible diets (Fig. 3C). The average dietary protein content of the diets selected during both fall and spring (22% ± 6%) was within that range and supports the hypothesis that bears selected foods in proportions that optimized their macronutrient intake.

Bears strongly preferred lipids over carbohydrates to reduce the protein content of the diet, but they used both lipids and carbohydrates when both were offered (Table 2). When lipids were not available freely, bears used carbohydrates as efficiently as lipids for maintenance and gain (Figs. 3A and 3B). Estimated growth rates did not differ when bears consumed high-lipid or high-carbohydrate diets as long as dietary protein content and energy intake were the same ($F_{1,8} = 2.34$, $P = 0.16$). Carbohydrate and lipid content in the preferred diets varied between seasons, but lipids provided 53% ± 7% of the dry matter and 73% ± 3% of the metabolizable energy in the preferred fall diets when protein, carbohydrates, and lipids were available ad libitum. Carbohydrates in the preferred spring and fall diets provided 17% ± 7% of the metabolizable energy (Table 2). When carbohydrates were not available, bears consumed diets in which up to 80% ± 3% of metabolizable energy (61% ± 5% of dry matter intake) came from lipids (Table 2; Fig. 2). Bears selected more lipids during the fall than during the spring ($t_2 = 5.89$, $P = 0.03$; 37% more lipid dry matter and 20% more lipid energy), but differences were not detected in protein or carbohydrate selection (protein $t_2 = -3.36$, $P = 0.08$; carbohydrates $t_2 = -1.71$, $P = 0.23$).

Bears offered ad libitum diets consumed up to 58,195 kcal of digestible energy/day (1,087 kcal $kg^{-0.75}$ day^{-1}, or 17.6 times the carnivore basal metabolic rate) and gained as much as 4.1 kg/day. Average maximum daily intake as a percent of body mass increased as the digestible energy content of the diet decreased, but bears maintained a constant level of energy intake across an 8-fold difference in dietary energy density ($t_3 = 1.18$, $P = 0.32$; Fig. 4). On average, bears consumed 30,576 ± 8,510 kcal of digestible energy/day in the fall (596 ± 132 kcal $kg^{-0.75}$ day^{-1}, or 9.6 ± 2.1 times the carnivore basal metabolic rate) and 24,072 ± 1,973 kcal of digestible energy/day (536 ± 45 kcal $kg^{-0.75}$ day^{-1}, or 8.7 ± 0.7 times the carnivore basal metabolic rate) in the spring.

Discussion

Brown bears were able to regulate their selection of foods to create mixed diets that maximized energy intake, optimized macronutrient intake, and, therefore, maximized mass gain per unit of energy intake. Brown bears are clearly energy maximizers because of the need to accumulate large fat reserves for hibernation, seasonal fasting, and reproduction, and the lack of any significant predation risk while foraging, which would select against obesity. The levels of energy intake observed in this and other studies when brown bears were given ad libitum food (Fig. 4) are some of the highest measured in mammals and birds, exceeding Kirkwood's (1983) estimated maximum metabolizable energy intake of 406 kcal $kg^{-0.72}$ day^{-1}. However, brown bears also must optimize macronutrient intake to be efficient energy-storage maximizers. Brown bears appeared to follow at least 3 rules in dietary selection: maximize energy intake while optimizing dietary protein content; select lipids over digestible carbohydrates when both are available to reduce dietary protein and maximize food

Table 2.—Average macronutrient selection (± *SD*) during ad libitum feeding trials of captive brown bears (*Ursus arctos*).

Diet items	% of dry matter			% of metabolizable energy[a]		
	Protein	Carbohydrate[b]	Lipid	Protein	Carbohydrate	Lipid
Fall						
Salmon, apples, beef fat	16 ± 6	26 ± 6	48 ± 1	11 ± 4	18 ± 4	71 ± 1
Beef, bread, pork fat	24 ± 5	15 ± 15	58 ± 10	15 ± 2	9 ± 9	76 ± 7
Salmon, salmon oil	31 ± 3	0	61 ± 5	20 ± 3	0	80 ± 3
Salmon, apples[c]	19 ± 3	52 ± 3	10 ± 2	21 ± 4	57 ± 5	22 ± 3
Spring						
Salmon, apples, beef fat	22 ± 6	29 ± 4	35 ± 2	18 ± 6	23 ± 3	59 ± 3

[a] Metabolizable energy calculated using Atwater specific factors for meat protein (4.27 kcal/g), fruit protein (3.36 kcal/g), grain protein (4.05 kcal/g), fruit digestible carbohydrate (4.00 kcal/g), grain digestible carbohydrate (4.20 kcal/g), meat lipid (9.03 kcal/g), fruit lipid (8.37 kcal/g), and grain lipid (8.37 kcal/g—Merrill and Watt 1973).

[b] Digestible carbohydrate, calculated by 100 − (protein + fat + total dietary fiber + ash).

[c] From Robbins et al. (2007), dry matter and metabolizable energy calculated using food values from this study.

energy density; and if lipids are not available or cannot be as efficiently exploited, use digestible carbohydrates to optimize dietary protein.

High- or low-protein diets consumed by brown bears decreased their rate of gain per unit of energy intake (Robbins et al. 2007; current study; Fig. 2). Both extremes in protein intake have undesirable metabolic consequences that likely provide multiple physiological mechanisms for sensing and regulating dietary protein intake to an optimum level (Metges and Barth 2000). Too little protein results in protein deficiency, reduced growth, and dietary-induced thermogenesis, whereas too much protein may contribute to diabetes, kidney disease,

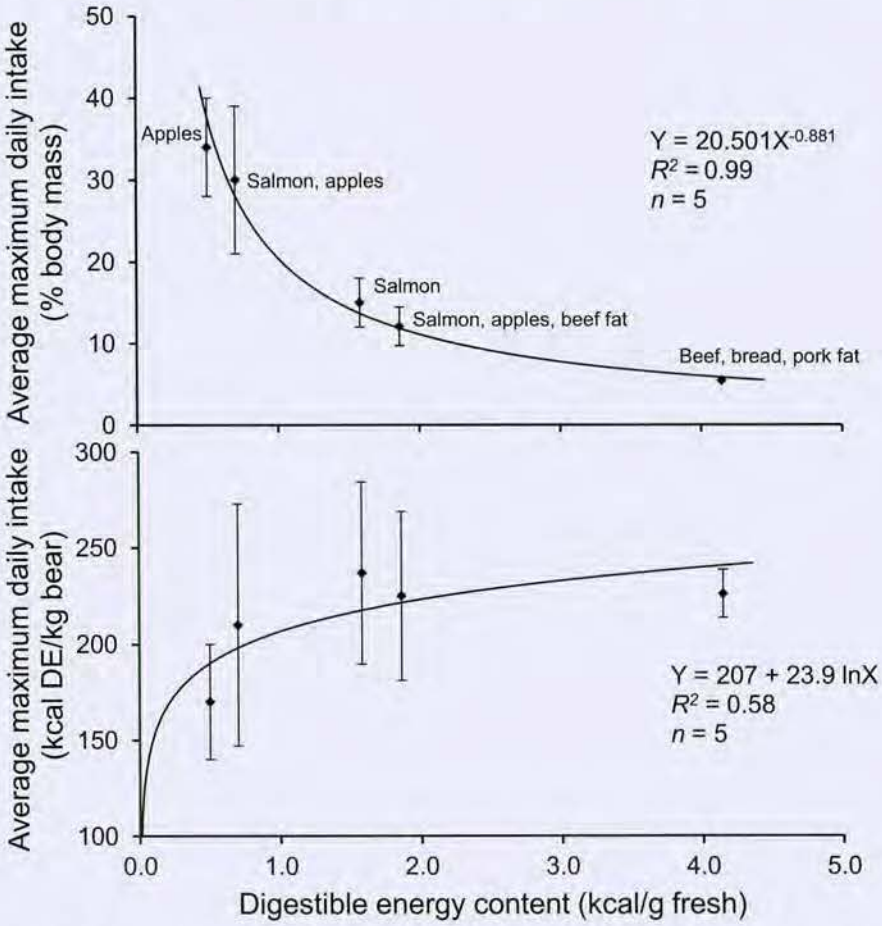

Fig. 4.—Average maximum daily intake by captive brown bears (*Ursus arctos*) consuming ad libitum apples (Welch et al. 1997); salmon and apples (Robbins et al. 2007); salmon (Hilderbrand et al. 1999); salmon, apples, and beef fat (current study); beef, bread, and pork fat (current study); and salmon and salmon oil (current study). Although digestible energy content of diets varied, average maximum daily digestible energy intake per kilogram was not significantly different between diets ($t_3 = 1.178$, $P = 0.3238$).

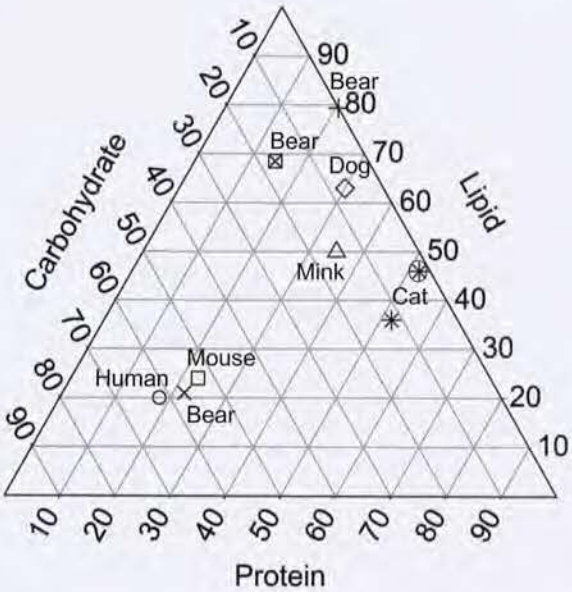

Fig. 5.—Average daily macronutrient selection (% of metabolizable energy) by captive brown bears (*Ursus arctos*) in comparison to other species when given ad libitum access to foods providing differing amounts of protein, carbohydrate, and lipids. Bears were given choices between salmon and salmon oil (+); salmon, apples, and beef fat and beef, bread, and pork fat (⊠); and salmon and apples (×). Dogs (*Canis lupus familiaris*, ◇—Hewson-Hughes et al. 2013), laboratory mice (□—Smith et al. 2000; Sørensen et al. 2008), mink (*Neovison vison*, Δ—Mayntz et al. 2009), and domestic cats (*Felis catus*,*—Hewson-Hughes et al. 2011) were each given multiple semisynthetic formulated diets varying in either protein, carbohydrate, and lipid content (dogs, mice, and domestic cats), protein and carbohydrate content (mice), or protein and lipid content (mink). Macronutrient selection of feral cats (⊛—Plantinga et al. 2011) was determined based on food habits of free-roaming feral cats. Humans (*Homo sapiens*, ○—Simpson et al. 2003) were given a buffet of common breakfast, lunch, dinner, and snack foods ranging in protein, carbohydrate, and lipid content. The carbohydrate content of the domestic mink diet was set at 15%, and therefore does not necessarily represent either the preferred carbohydrate or fat choice if both were freely available. The mouse value represents macronutrient selection by nonobese mouse strains, which we believe would select diets most similar to wild mice.

increased calcium excretion, and metabolic acidosis. Thus, the ability of brown bears to consistently select the optimum level of dietary protein when foods having all 3 macronutrients are available (current study) and to overeat nonprotein energy in an attempt to meet their protein requirement when protein is inadequate (Felicetti et al. 2003) suggests that brown bears are similar to other species that prioritize dietary protein (i.e., "protein leverage"—Simpson and Raubenheimer 2007:6; Sørensen et al. 2008; Felton et al. 2009).

The high level of lipid consumption by brown bears (all-season mean 68% ± 9% of metabolizable energy) is greater than that of any other species studied thus far, including domestic dogs (*Canis lupus familiaris*, $t_6 = 3.76$, $P = 0.0094$; Fig. 5). However, the closely related polar bear is well known for preferentially consuming fat when feeding on marine mammals (Stirling and McEwan 1975; Best 1985; Miller et al. 2012). Best (1976, 1985) offers some of the only information on macronutrient selection by polar bears, but these accounts are somewhat contradictory. Best (1976:64) reported that polar bears "may consume up to 80% of the total food intake (as blubber), the remainder (i.e., 20%) being protein." However, Best (1985:1035) later stated that captive polar bears selected a diet that was 20% ± 2% meat with the rest being blubber, which represents a dietary protein content of as little as 4% on a dry matter basis and is atypical of other carnivores and omnivores (i.e., 20 g meat/100 g diet × 0.30 × 0.73, where dry matter content of meat is 30% and protein is 73% of the dry matter [Best 1985; Robbins 1993]). Best (1985:1035) further compared the level of dietary meat consumed by polar bears to the "protein requirement for the dog [of] 18 to 20%," suggesting that polar bears and dogs had a similar protein requirement. If the 2 polar bears in Best's (1985) study consumed a diet of 20% protein, rather than 20% meat, their diet would have been consistent with the macronutrient selection of brown bears in our study.

Irrespective of what the actual protein and fat intake of polar bears was in Best's (1976) study, the preference for fat in polar bear diets has been explained as a means to conserve water by minimizing nitrogen excretion associated with excess protein consumption (Nelson 1983). An equally plausible explanation is that polar bears are maximizing energy intake by ingesting lipids, optimizing macronutrient intake by using lipids to reduce excess protein, and thereby maximizing mass gain per unit of energy intake. Similarly, failure to recognize the importance of macronutrient optimization and the energetic costs of nutrient metabolism in determining energy expenditure and diets of polar bears can produce erroneous estimates of the ability of polar bears to live successfully on terrestrial diets during ice-free times as global warming occurs (Dyck and Kebreab 2009; Rode et al. 2010).

Because bears prefer and efficiently use high-lipid foods, the importance of these foods should be recognized. Such foods include army cutworm moths (*Euxoa auxiliaris*) and whitebark pine nuts (*Pinus albicaulis*) for Yellowstone grizzly bears (*U. a. horribilis*) and ringed seals (*Pusa hispida*) and other marine mammals for polar bears (Stirling and McEwan 1975; Mattson et al. 1992; French et al. 1994). The high lipid content of these foods is not their only merit—they also contain protein concentrations similar to the levels preferred by brown bears in the current study (22% ± 6% of dry matter). For example, the dry matter of army cutworm moths contains 27% protein, whitebark pine nuts 21%, harp seals (*Pagophilus groenlandicus*) 21%, and adult ringed seals 29% (Stirling and McEwan 1975; Best 1985; French et al. 1994; White et al. 1998; Dyck and Morin 2011).

Although our study showed a preference of brown bears for high-lipid foods, ecological factors also should be considered when understanding bear diets. High-lipid foods are not available in many ecosystems and are decreasing in others (e.g., whitebark pine nuts in the northern Rocky Mountains [Kendall and Keane 2001]). Furthermore, even when high-lipid

foods are present, they may not always be selected. McLellan and Hovey (1995) observed that wild grizzly bears preferred high-carbohydrate berries to high-lipid whitebark pine nuts in their study in the northern Rockies. This presumably occurred because the net rate of energy consumption when feeding on berries was higher than when feeding on pine nuts. Because both high-lipid and high-carbohydrate foods can be important to bears, understanding the diets of wild bears will require careful consideration of the complex foraging relationships that occur in the wild.

Brown bears exhibited macronutrient-selection characteristics of both carnivores and omnivores. Although classified in the order Carnivora, brown bears selected protein (17% ± 4% of metabolizable energy) at a much lower level than domestic and feral cats (*Felis catus*, 52% of metabolizable energy [Hewson-Hughes et al. 2011; Plantinga et al. 2011]) and domestic mink (*Neovison vison*, 35% of metabolizable energy [Mayntz et al. 2009]), but much closer to levels chosen by other omnivores, including humans (*Homo sapiens*, ~15% of total energy [Simpson et al. 2003]), mice (~25% of metabolizable energy [Sørensen et al. 2008]), spider monkeys (*Ateles chamek*, ~13% of total energy [Felton et al. 2009]), and fruit-eating gorillas (*Gorilla beringei*, 19% of total energy [Rothman et al. 2011]). However, unlike other omnivores that prefer high-carbohydrate, low-lipid diets (Smith et al. 2000; Simpson et al. 2003; Sørensen et al. 2008; Fig. 5), brown bears and dogs shared the carnivore's preferences for low-carbohydrate, high-lipid diets. Examination of the only data available for other omnivores also suggests a wide range of lipid preference that, in mice, ranged from 26% to 83% of metabolizable energy and was directly related to their propensity for obesity (Smith et al. 2000). Laboratory mice artificially selected for obesity chose diets with macronutrient profiles similar to those of brown bears that have been evolutionarily selected for obesity.

In summary, brown bears show macronutrient-selection strategies that both unite them with and set them apart from other species. Energy maximization and macronutrient balancing are both important foraging strategies for brown bears. Although lipids are highly preferred, lipids and digestible carbohydrates can both be used by brown bears with equal efficiency to adjust the protein content of their diet to an optimum level that maximizes mass gain. Thus, dietary sources of lipids and digestible carbohydrates play an important role in determining the productivity of bears that extends beyond the role of these nutrients in providing energy (Robbins et al. 2007; Robbins et al. 2012a, 2012b).

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Literature Cited

Best, R. C. 1976. Ecological energetics of the polar bear (*Ursus maritimus* Phipps 1774). M.S. thesis, University of Guelph, Guelph, Ontario, Canada.

Best, R. C. 1985. Digestibility of ringed seals by the polar bear. Canadian Journal of Zoology 63:1033–1036.

Cotter, S. C., S. J. Simpson, D. Raubenheimer, and K. Wilson. 2011. Macronutrient balance mediates trade-offs between immune function and life history traits. Functional Ecology 25:186–198.

Dyck, M. G., and E. Kebreab. 2009. Estimating the energetic contribution of polar bear (*Ursus maritimus*) summer diets to the total energy budget. Journal of Mammalogy 90:585–593.

Dyck, M. G., and P. Morin. 2011. In vivo digestibility trials of a captive polar bear (*Ursus maritimus*) feeding on harp seal (*Pagophilus groenlandicus*) and arctic charr (*Salvelinus alpinus*). Pakistan Journal of Zoology 43:759–767.

Felicetti, L. A., C. T. Robbins, and L. A. Shipley. 2003. Dietary protein content alters energy expenditure and composition of the mass gain in grizzly bears (*Ursus arctos horribilis*). Physiological and Biochemical Zoology 76:256–261.

Felton, A. M., et al. 2009. Protein content of diets dictates the daily energy intake of a free-ranging primate. Behavioral Ecology 20:685–690.

Fortin, J., S. D. Farley, K. D. Rode, and C. T. Robbins. 2007. Dietary and spatial overlap between sympatric ursids relative to salmon use. Ursus 18:19–29.

French, S. P., M. G. French, and R. R. Knight. 1994. Grizzly bear use of army cutworm moths in the Yellowstone Ecosystem. Bears: Their Biology and Management 9:389–399.

Gende, S. M., T. P. Quinn, R. Hilborn, A. P. Hendry, and B. Dickerson. 2004. Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice. Oikos 104:518–528.

Hewson-Hughes, A. K., et al. 2013. Geometric analysis of macronutrient selection in breeds of the domestic dog, *Canis lupus familiaris*. Behavioral Ecology 24:293–304.

Hewson-Hughes, A. K., V. L. Hewson-Hughes, A. T. Miller, S. R. Hall, S. J. Simpson, and D. Raubenheimer. 2011. Geometric analysis of macronutrient selection in the adult domestic cat, *Felis catus*. Journal of Experimental Biology 214:1039–1051.

Hilderbrand, G. V., S. G. Jenkins, C. C. Schwartz, T. A. Hanley, and C. T. Robbins. 1999. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Canadian Journal of Zoology 77:1623–1630.

Hobson, K. A., I. Stirling, and D. S. Andriashek. 2009. Isotopic homogeneity of breath CO_2 from fasting and berry-eating polar bears: implications for tracing reliance on terrestrial foods in a changing Arctic. Canadian Journal of Zoology 87:50–55.

Joshi, A. R., D. L. Garshelis, and J. L. D. Smith. 1997. Seasonal and habitat-related diets of sloth bears in Nepal. Journal of Mammalogy 78:584–597.

Kendall, K. C., and R. E. Keane. 2001. Whitebark pine decline: infection, mortality, and population trends. Pp. 221–242 in Whitebark pine communities: ecology and restoration (D. F. Tomback, S. F. Arno, and R. E. Keane, eds.). Island Press, Washington, D.C.

Kirkwood, J. K. 1983. A limit to metabolisable energy intake in mammals and birds. Comparative Biochemistry and Physiology, A. Physiology 75:1–3.

Kovach, A. I., and R. A. Powell. 2003. Effects of body size on male mating tactics and paternity in black bears, *Ursus americanus*. Canadian Journal of Zoology 81:1257.

MacArthur, R. H., and E. R. Pianka. 1966. On the optimal use of a patchy environment. American Naturalist 100:603–609.

Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark-pine seed crops. Journal of Wildlife Management 56:432–442.

Mayntz, D., et al. 2009. Balancing of protein and lipid intake by a mammalian carnivore, the mink, *Mustela vison*. Animal Behaviour 77:349–355.

McLellan, B. N., and F. W. Hovey. 1995. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. Canadian Journal of Zoology 73:704–712.

Merrill, A. L., and B. K. Watt. 1973. Energy value of foods: basis and derivation, revised. Agriculture Handbook 74. United States Department of Agriculture, Washington, D.C.

Metges, C. C., and C. A. Barth. 2000. Metabolic consequences of a high dietary protein intake in adulthood: assessment of the available evidence. Journal of Nutrition 130:886–889.

Miller, W., et al. 2012. Polar and brown bear genomes reveal ancient admixture and demographic footprints of past climate change. Proceedings of the National Academy of Sciences 109:2382–2390.

Nelson, R. A., G. E. Folk, Jr., E. W. Pfeiffer, J. J. Craighead, C. J. Jonkel, and D. L. Steiger. 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. Bears: Their Biology and Management 5:284–290.

Plantinga, E. A., G. Bosch, and W. H. Hendriks. 2011. Estimation of the dietary nutrient profile of free-roaming feral cats: possible implications for nutrition of domestic cats. British Journal of Nutrition 106:35–48.

Pritchard, G. T., and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology 68:1645–1651.

Raubenheimer, D., S. J. Simpson, and D. Mayntz. 2009. Nutrition, ecology and nutritional ecology: toward an integrated framework. Functional Ecology 23:4–16.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Academic Press, San Diego, California.

Robbins, C. T., M. Ben-David, J. K. Fortin, and O. L. Nelson. 2012a. Maternal condition determines birth date and growth of newborn bear cubs. Journal of Mammalogy 93:540–546.

Robbins, C. T., J. K. Fortin, K. D. Rode, S. D. Farley, L. A. Shipley, and L. A. Felicetti. 2007. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. Oikos 116:1675–1682.

Robbins, C. T., C. Lopez-Alfaro, K. D. Rode, Ø. Tøien, and O. L. Nelson. 2012b. Hibernation and seasonal fasting in bears: the energetic costs and consequences for polar bears. Journal of Mammalogy 93:1493–1503.

Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. Biological Conservation 133:70–80.

Rode, K. D., J. D. Reist, E. Peacock, and I. Stirling. 2010. Comments in response to "Estimating the energetic contribution of polar bear (*Ursus maritimus*) summer diets to the total energy budget" by Dyck and Kebreab (2009). Journal of Mammalogy 91:1517–1523.

Rode, K. D., and C. T. Robbins. 2000. Why bears consume mixed diets during fruit abundance. Canadian Journal of Zoology 78:1640–1645.

Rothman, J. M., D. Raubenheimer, and C. A. Chapman. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. Biology Letters 7:847–849.

SAS Institute Inc. 1998. SAS user's guide: statistics. Version 6.12. SAS Institute Inc., Cary, North Carolina.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Simpson, S. J., R. Batley, and D. Raubenheimer. 2003. Geometric analysis of macronutrient intake in humans: the power of protein? Appetite 41:123–140.

Simpson, S. J., and D. Raubenheimer. 2007. The protein leverage hypothesis in human obesity. Annals of Nutrition and Metabolism 51:6–36.

Simpson, S. J., and D. Raubenheimer. 2009. Macronutrient balance and lifespan. Aging 1:875–880.

Simpson, S. J., and D. Raubenheimer. 2012. The nature of nutrition: a unifying framework from animal adaptation to human obesity. Princeton University Press, Princeton, New Jersey.

Simpson, S. J., R. M. Sibly, K. P. Lee, S. T. Behmer, and D. Raubenheimer. 2004. Optimal foraging when regulating intake of multiple nutrients. Animal Behaviour 68:1299–1311.

Smith, B. K., P. K. Andrews, and D. B. West. 2000. Macronutrient diet selection in thirteen mouse strains. American Journal of Physiology—Regulatory, Integrative and Comparative Physiology 278:797–805.

Sørensen, A., D. Mayntz, D. Raubenheimer, and S. J. Simpson. 2008. Protein-leverage in mice: the geometry of macronutrient balancing and consequences for fat deposition. Obesity 16:566–571.

Steinmetz, R., D. L. Garshelis, W. Chutipong, and N. Seuaturien. 2013. Foraging ecology and coexistence of Asiatic black bears and sun bears in a seasonal tropical forest in Southeast Asia. Journal of Mammalogy 94:1–18.

Stirling, I., and E. McEwan. 1975. The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behavior. Canadian Journal of Zoology 53:1021–1027.

Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. Ecology 78:1105–1119.

White, D., Jr., K. C. Kendall, and H. D. Picton. 1998. Seasonal occurrence, body composition, and migration potential of army cutworm moths in northwest Montana. Canadian Journal of Zoology 76:835–842.

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