Foods and nutritional components of diets of black bear in Rocky Mountain National Park, Colorado

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Abstract: We used scat analysis to determine diets and relative nutritional values of diets for black bears (*Ursus americanus* Pallas, 1780) in Rocky Mountain National Park, Colorado, from 2003 to 2006, and compared foods consumed and nutritional components to identify important sources of fecal gross energy (GE), crude fat (CF), and fecal nitrogen (FN) in annual and seasonal diets. Patterns of use of food classes followed typical seasonal patterns for bears, although use of animal matter was among the highest reported (>49% annually). Use of animal matter increased after spring, although crude protein levels in bear diets were always >25%. GE was typically lowest for grasses and other herbaceous plants and highest for ants and ungulates; FN was strongly positively related to most animal sources, but negatively correlated with vegetative matter; and CF showed the strongest positive relationship with ungulates and berries, with the latter likely influenced by the presence of seeds. Compared with historic data (1984–1991), contemporary diets included substantially greater prevalence of anthropogenic foods, which likely contributed to increases in size, condition, and productivity of the contemporary bear population. Management strategies are needed to increase quantity and quality of natural foods while minimizing dependence on anthropogenic sources.

Résumé : Une analyse des fèces nous a servi à déterminer le régime alimentaire et la valeur nutritionnelle relative de ce régime chez des ours noirs (*Ursus americanus* Pallas, 1780) dans le parc national des Montagnes Rocheuses, Colorado, de 2003 à 2006; nous avons comparé les aliments consommés et les composantes nutritives afin d'identifier les sources importantes d'énergie fécale brute (GE), de lipides bruts (CF) et d'azote fécal (FN) dans les régimes alimentaires annuels et saisonniers. Les patrons d'utilisation des diverses classes d'aliments suivent les patrons saisonniers typiques des ours, bien que le taux d'utilisation de matière animale soit parmi les plus élevés (>49 % sur une base annuelle) jamais observés. L'utilisation de matière animale augmente après le printemps bien que les concentrations brutes de protéines soient toujours >25 %. Les valeurs de GE sont typiquement minimales pour les herbes et les autres plantes herbacées et maximales pour les fourmis et les ongulés; il y a une forte corrélation positive entre FN et la plupart des sources alimentaires animales et une corrélation négative avec la matière végétale; la plus forte relation positive existe entre CF et les ongulés et les baies, dans ce dernier cas vraisemblablement influencée par la présence de graines. Par comparaison aux données du passé (1984–1991), les régimes alimentaires actuels comprennent une fréquence nettement plus élevée d'aliments d'origine humaine, ce qui contribue vraisemblablement à l'augmentation de la taille, de la condition et de la productivité de la population présente d'ours. Il faudrait établir des stratégies de gestion pour augmenter la quantité et la qualité des aliments naturels, tout en minimisant la dépendance de sources anthropiques.

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Introduction

Diets of black bears (*Ursus americanus* Pallas, 1780; hereafter bear) vary geographically depending on foods available to bears (Pelton 2003). Knowledge of foods utilized by local bear populations provides insight into condition, reproductive rates, and habitat selection of bears, aiding effective management of these populations. One of the most commonly used techniques for assessing food habits is scat analysis. Food items from scats are identified and related to diets through frequency, relative density, or volume (e.g., Raine and Kansas 1990; Hellgren 1993; Kasbohm et al. 1995). Correction factors have also been developed for common food items to account for differences in digestibilities (Hewitt and Robbins 1996), with the use of these corrected values allowing for more accurate identification of important foods.

Identification of foods consumed does not necessarily indicate which foods are most beneficial to bears, whereas knowledge of nutritional gains from foods provides insight

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into which supply the greatest gains of energy and other key nutrients (Gluesing and Field 1986). The majority of past work has attempted to delineate these relationships by relating nutritional components of selected foods to quantities consumed (e.g., Elowe and Dodge 1989; Kasbohm et al. 1995). However, nutritional composition of plant species can vary substantially from plant to plant and even within the same plant (Holechek et al. 2004). Alternatively, nutritional components of fecal material from species with ruminant and monogastric digestive systems have been used to assess dietary quality (Studier et al. 1994; Hodgman et al. 1996; Magomedov et al. 1996; Felicetti et al. 2000; Codron et al. 2006). Fecal indices assume that as dietary intake of measured nutrients increases, so do fecal levels of those nutrients (Codron et al. 2006). This is particularly true for monogastrics, such as bears, because of higher dietary requirements and a digestive system that can process only highly digestible nutrients such as proteins, lipids, and simple sugars (Pritchard and Robbins 1990; Robbins 1993), which are highly digestible (Brody and Pelton 1988; Pritchard and Robbins 1990). For example, fecal nitrogen (FN) levels have been shown to vary directly with dietary nitrogen intake in several free-ranging omnivores as diverse as bats (Studier et al. 1994), baboons (Codron et al. 2006), and bears (Brody and Pelton 1988). Although factors other than dietary intake may affect FN levels, such as precipitation of proteins by tannins (Robbins 1993) that increase FN content, most simple monogastrics avoid such forages and presence of these forages can be identified in diets to determine any potential confounding effects. Other key nutrients for bears, such as lipids and energy, are less studied, but limited data indicate that fecal levels positively correlate with intake levels, although (like FN) fecal concentrations are lower owing to high digestibilities (Brody and Pelton 1988).

Thus, even though food sources have a variety of digestibilities with respect to nutritional components (Pritchard and Robbins 1990), estimates derived from consumed foods (i.e., scats and stomach content) likely represent as a minimum relative levels of nutritional components, and thereby reflect quality of diets consumed (Brody and Pelton 1988; Magomedov et al. 1996; Clark et al. 2003; Codron et al. 2006). Although limited evidence suggests that nutrient assimilation rates can vary seasonally in bears (Brody and Pelton 1988), this may simply reflect differences in nutrient availability (Pritchard and Robbins 1990), and regardless, differences are slight (Brody and Pelton 1988). Knowing which dietary items provide greatest nutrient gains to bears is important because consumption of energy-rich foods is critical for bears given their need to accrue large stores of fat for hibernation (Pelton 2003). High-energy foods include a variety of soft-mast-producing plants, as well as fat and protein-rich food sources such as hard mast, insects, and animal matter (Swenson et al. 1999; Rode and Robbins 2000; Inman and Pelton 2002), and high-protein diets can also result in increased mass gains and fecundity in bears (Tate and Pelton 1983; McLean and Pelton 1990; Beckmann and Berger 2003*a*).

Studies of food habits of bears from 1984 to 1991 in Rocky Mountain National Park (RMNP), Colorado, indicated greater use of animal matter compared with other localities (L.C. Zeigenfuss, United State Geological Survey, 2001 unpublished report), although direct comparisons with other studies was difficult because food habits were not assessed volumetrically, thus precluding the application of correction factors to more accurately represent foods consumed. RMNP's bear population is unique in that it is one of the highest elevation populations of bears in the United States, and such high elevations result in a substantially shorter growing season and a lack of hard-mast crops utilized by bears in other localities. These factors were believed to be the cause of the small size of bears (adult male = 74 kg, adult female = 60 kg; Baldwin 2008) reported in RMNP historically (1984–1991). However, recent observations (2003–2006, hereafter contemporary) indicated increased size (adult male = 99 kg, adult female = 68 kg; Baldwin 2008) and condition (mean body fat females — historic = 15%, contemporary = 24%; Baldwin and Bender 2009) over historic data, a result most parsimoniously related to changes in level of nutrition.

We hypothesized that contemporary diets of black bears would exhibit greater use of animal foods than in most other bear populations, that use of animal foods would be highest in summer and autumn, and that these animal foods would be significant sources of protein, fat, and energy. We predicted that contemporary diets would differ from historic diets given the increase in size and nutritional condition of bears over the last 15–20 years. Furthermore, given this increase in condition in bears, we predicted greater use of anthropogenic foods for the contemporary population given the high nutrient content of these foods (Stringham 1989). If correct, these predictions would underscore the importance of animal matter in diets of black bears in RMNP, and would indicate a need to modify current management of black bears in RMNP to reduce potential human–bear conflicts that are likely to arise when bears heavily utilize anthropogenic foods (Beckmann and Berger 2003*b*).

Study area

RMNP is a 1080 km^2 biosphere reserve located in the Rocky Mountain Front Range of north-central Colorado. Topography in RMNP was shaped by glaciations, and consists of high mountainous peaks interspersed with small subalpine meadows, lakes, streams, glaciers, and tundra at higher elevations. Elevations range from 2400 to 4345 m. The continental divide bisects RMNP, creating different climatic patterns and vegetation types to the east and west. Eastern RMNP is drier, with precipitation averaging 35.1 cm in the town of Estes Park, while western RMNP is more mesic, with precipitation averaging 50.8 cm in the town of Grand Lake. Seventy-five percent of precipitation falls from April to September. In Estes Park, mean daily high temperatures range from 7.2 °C in February to 27.8 °C in July, while in Grand Lake, mean daily high temperatures range from 0.0 °C in December and January to 23.9 °C in July.

Vegetation in RMNP consisted of >700 plant species. Community composition varied with more productive communities found on western slopes and at higher elevations (Beidleman et al. 2000). Montane forests and valleys west of the continental divide were comprised primarily of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Wats.)

and aspen (*Populus tremuloides* Michx.) interspersed with bunchgrass and sedge-dominated herbaceous meadows. Montane forests on the eastern slope included the same species, although drier sites were often dominated by ponderosa pine (*Pinus ponderosa* P. & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco). Subalpine habitats varied less between western and eastern slopes and were dominated by Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) with limber pine (*Pinus flexilis* James) occasionally present. Elevations above timberline (~3500 m) were dominated by tundra and bare rock. Below the treeline, wetland and riparian areas were composed of a variety of species but were dominated by dense stands of spruce–fir and aspen in forested areas (Salas et al. 2005).

Common mammalian food sources for bears included mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), elk (*Cervus elaphus* L., 1758), snowshoe hare (*Lepus americanus* Erxleben, 1777), deer mouse (*Peromyscus maniculatus* (Wagner, 1845)), red squirrel (*Tamiasciurus hudsonicus* (Erxleben, 1777)), and yellow-bellied marmot (*Marmota flaviventris* (Audubon and Bachman, 1841)). Common insect foods included a wide variety of ants (order Hymenoptera), beetles (order Coleoptera), and hornets (order Hymenoptera). Anthropogenic food sources were also available around campsites and residential areas. Many dumpsters inside and outside the RMNP boundary were bear proof, although not all. These dumpsters, along with foods carried by hikers and bird feeders found in residential areas, provided additional foods for bears in RMNP.

Materials and methods

Food habits

We collected bear scats when encountered during associated field activities (i.e., telemetry, focal animal observations, and vegetation surveys; Baldwin 2008) from summer 2003 to autumn 2006, and recorded location, date collected, and approximate age (<1 week, 1–4 weeks, >4 weeks) of each scat. We followed guidelines for the care of animals as required by the Canadian Council on Animal Care, and all activities were in compliance with New Mexico State University Institutional Animal Care and Use Committee permit No. 2002-26. For analysis, we soaked each fecal sample in water and antibacterial soap overnight. We then rinsed samples in hot and cold water for 5 min over 2.38 and 1 mm soil screens. We spread remaining materials on a tray, mixed thoroughly, and randomly selected 10%–33% of the remaining food items for further analysis (Hewitt and Robbins 1996). We then submerged these materials in water to allow easier separation of food items and placed remains into 1 of 10 categories including grasses, other herbaceous plants (hereafter, herbaceous), berries, hard mast, ants, other insects (hereafter, insects), small mammals, ungulates, garbage, and nonfood items (for further description see Table 1). We identified plant materials using reference collections and plant identification keys (i.e., Beidleman et al. 2000), while small mammals and ungulates were identified from hair and bone remains using reference collections and hair keys (Moore et al. 1974). Once we completed identification, we squeezed excess water from food items and estimated volume using water displacement in a graduated cylinder (Hewitt and Robbins 1996).

We applied correction factors (grass = 0.26; herbaceous = 0.26; berries = 0.93; hard mast = 1.5; ants = 1.74; insects = 1.1; small mammals = 4.0; neonate ungulates = 1.5; other ungulates = 3.0) to volumetric estimates of food items to account for differing digestibilities of food items (Hewitt and Robbins 1996; Bunnell 2000). No correction factors were available for garbage items (i.e., plastic, paper, rubber, aluminum foil). Therefore, we excluded scats containing these items from analyses involving correction factors given that even for food items in which we had established correction factors, corrected volumes might be inaccurate given the unknown volume of anthropogenic foods consumed. When we collected multiple scats believed to have been deposited from the same individual from a single feeding bout, we averaged these samples with the mean serving as a single observation.

We determined seasonal composition of bear diets by placing collected scats into spring (May–June), summer (July–August), and autumn (September–November) categories. We used the median date between date of collection and last day of approximate age (either 1 or 4 weeks) for scats where date of deposit was unknown. We did not use any scats in seasonal analyses that were aged >4 weeks given the high uncertainty about the date of deposit. We compared diets across seasons and among years for both uncorrected and corrected volumetric percentages using Kruskal–Wallis tests (Zar 1999).

Scats were also collected throughout the year during the historic period, with scats analyzed at the Composition Analysis Laboratory, Fort Collins, Colorado (McCutchen 1996). Food items were classed as grass, herbaceous, berry, insect, and animal matter; we could not further define insect (i.e., ants and other insects) and animal (i.e., ungulates and small mammals) classes given the lack of specificity for these food items from historic scats. We compared the frequency of the primary food item per scat (i.e., food item with the greatest percent occurrence in each scat; Rosas-Rosas et al. 2003) between the historic and the contemporary periods to assess shifts in dietary constituents across time; we were not able to compare volumetric measures for the historic period because such data were not collected. We used Fisher's exact test (Zar 1999) for the above comparison, and Fisher's exact tests with a Bonferroni correction (α = 0.01) for multiple comparisons (Zar 1999). Because collection dates were not recorded historically, we could only do historical versus contemporary comparisons for annual diets. We also compared the number of scats with anthropogenic food sources to the total number of scats sampled using Fisher's exact test (Zar 1999) for both the historic and the contemporary periods in RMNP to assess differences in utilization of these food sources. This analysis was conducted separately from the other frequency comparisons, given a larger available data set that included the presence of anthropogenic foods for the historic period.

Nutritional analysis

Before soaking scats, we manually homogenized scats and collected a subsample from each scat for use in nutritional analyses to determine levels of gross energy (GE; calories/

Table 1. Description of dietary classes used to categorize diets of black bears (*Ursus americanus*) in Rocky Mountain National Park, Colorado, from 2003 to 2006.

Scat item	Description
Grass	All monocots including grasses, sedges, and rushes
Herbaceous	All forbs and leafy plant material but primarily blueberries (genus *Vaccinium* L.), dandelion (genus *Taraxacum* G.H. Weber ex Wiggers), and cow parsnip (*Heracleum maximum* Bartr.)
Berries	All berries but primarily *Vaccinium* spp., currants (genus *Ribes* L.), russet buffaloberries (*Shepherdia canadensis* (L.) Nutt.), bearberries (*Arctostaphylos uva–ursi* (L.) Spreng.), and Virginia chokecherries (*Prunus virginiana* L.)
Hard mast	Sunflower seeds from bird feeders
Ants	All ant species
Insects	All insects other than ants but primarily wasps
Small mammals	Members of Rodentia and Lagomorpha
Ungulates	Mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*)
Garbage	Includes primarily plastic, paper, rubber, and aluminum foil
Nonfoods	Primarily woody debris, soil, and sand

g, where 1 calorie = 4.184 J), crude fat (CF; %), and FN (%) for each scat. We determined GE using a bomb calorimeter (IKA C5000 model), FN by a carbon/nitrogen analyzer (Leco Truspec model), and CF by ether extract using a Goldfisch (Labconco) apparatus. In addition, we determined total ash for each sample to convert nutritional components from dry matter to an organic matter basis. All chemical nutritional analyses were conducted by The Wildlife Habitat Nutrition Laboratory, Pullman, Washington. We compared seasonal values using procedures described above for food composition analyses. We also used Pearson's product-moment correlation (Zar 1999) to relate corrected volumetric percentages of food items in scats to GE, CF, and FN. We assessed outliers using residual plots (Zar 1999), and conducted analyses annually and seasonally to assess the seasonal influence of food items on nutritional components. Scats containing hard mast were not included in correlation analyses, as all hard mast was from anthropogenic sources, hard mast was observed in only 5 of 128 scats for which we had nutritional data, and because most of these scats were extreme outliers.

Results

Grasses (28%), berries (16%), and ants (16%) composed the largest percentage of bear diets in RMNP based on uncorrected fecal volume (Table 2). Collectively, vegetative matter made up 57.3% and animal matter made up 28.9% of annual bear diets, while garbage (5.2%) and nonfood items (8.2%) accounted for the rest. Seasonally, fecal volume for grasses ($H_2 = 20.2$, $p < 0.001$), ants ($H_2 = 5.3$, $p = 0.072$), and berries ($H_2 = 16.8$, $p < 0.001$) varied, whereas all other foods were similar ($H_2 \leq 3.3$, $p \geq 0.195$). Use of grasses declined seasonally, use of berries increased through autumn, and use of ants peaked during summer (Table 2). Fecal volume corrected for differential digestibility identified the same three primary food sources in bear diets annually, although ants became the primary food source (≥31.2%; Table 2). Corrected values indicated equivalent volumes of plant (51.0%) and animal (49.0%) food sources in RMNP bear diets. Corrected use of grasses ($H_2 = 21.8$, $p < 0.001$) again declined from spring through autumn, while consumption of berries ($H_2 = 10.1$, $p = 0.007$) and small mammals ($H_2 = 5.4$, $p = 0.068$) increased through autumn (Table 2).

Frequency of primary food items in scats differed (Fisher's exact test, $p < 0.0001$) between historic and contemporary samples, with greater frequency of insects (Fisher's exact test, $p < 0.001$) and less grass (Fisher's exact $p < 0.001$) in historical bear diets; no other food types varied (Fisher's exact test, $p \geq 0.060$) (Table 3). Scats containing anthropogenic food sources were 15.2 times (Fisher's exact test, $p < 0.0001$) more common in contemporary bear diets (mean = 14.2%; 17 of 120) than in historical bear diets (mean = 0.9%; 2 of 214). Because these foods were extremely difficult to identify (many human foods consist of leftover meat, etc., that leaves no distinct remains), this proportion likely significantly underestimates the true occurrence of such food items in black bear diets.

GE ($H_2 = 9.7$, $p = 0.008$) and CF ($H_2 = 4.9$, $p = 0.085$) content of bear scats differed across seasons, with GE (spring = 5441 calories (SE = 93 calories), summer = 5656 calories (SE = 60 calories), autumn = 5425 calories (SE = 112 calories); $p \leq 0.069$) and CF (spring = 4.8% (SE = 0.5%), summer = 6.2% (SE = 0.4%), autumn = 4.6% (SE = 0.6%); $p \leq 0.041$) being higher during summer than in spring or autumn, whereas spring and autumn did not differ (GE: $p = 0.909$; CF: $p = 0.749$). FN ($H_2 = 4.3$, $p \geq 0.679$) did not vary across seasons (spring = 4.1% (SE = 0.5%), summer = 4.4% (SE = 0.3%), autumn = 4.3% (SE = 0.7%)). GE was positively related to proportions of ants and ungulates in annual diets, while grasses and herbaceous food items were negatively related to GE (Table 4). Similar patterns were present for seasonal diets, except for ungulates during summer and autumn (Table 4).

CF levels in bear scats were negatively related to grasses but positively related to berry consumption annually (Table 4); this relationship for berries was particularly high during summer and autumn. Berries and ungulate biomass were positively related to CF in ≥1 season (Table 4), while consumption of insects (including ants) and small mammals was negatively associated with CF in ≥1 season.

FN was positively related to consumption of animal matter and indicated diets contained >25% crude protein (= 6.25 × nitrogen; Robbins 1993) in each season. Increasing amounts of grasses, herbaceous plants, and berries were associated with less FN in bear scats seasonally and annually (Table 4). Regardless of season, insects other than ants were consistently positively associated with FN values,

Table 2. Percent volume of items observed in fecal samples (uncorrected), as well as corrected values indicating percent diet composition of ingested foods (corrected), from black bears (*Ursus americanus*) in Rocky Mountain National Park, Colorado, from 2003 to 2006.

	Percent fecal volume (uncorrected)						Percent fecal volume (corrected)*					
	Annual (n = 120)	Spring (n = 32)	Summer (n = 56)	Autumn (n = 22)	H	p	Annual (n = 107)	Spring (n = 28)	Summer (n = 52)	Autumn (n = 18)	H	p
Grass	27.7	53.0a	22.5b	3.1c	20.2	<0.001	24.2	49.1a	7.5b	0.7c	21.8	<0.001
Herbaceous	11.2	9.8	12.5	10.3	0.9	0.629	7.2	8.4	5.9	7.6	0.1	0.959
Berries	16.1	5.3a	17.2b	36.0c	16.8	<0.001	16.8	5.8a	20.5b	31.6b	10.1	0.007
Hard mast	2.3	0.2	2.0	6.8	1.0	0.599	2.8	0.4	1.9	10.3	2.9	0.229
Ants	15.7	7.5a	23.9b	11.2a	5.3	0.072	31.2	21.6	40.3	24.7	2.0	0.376
Insects	3.2	1.5	4.3	3.5	3.3	0.195	6.1	3.7	6.6	11.1	2.5	0.281
Small mammals	3.9	3.7	2.4	9.5	1.8	0.413	5.0	0.0a	3.5a	14.0b	5.4	0.068
Ungulates	6.1	8.3	3.2	0.0	1.9	0.380	6.7	11.1	3.9	0.0	2.1	0.353
Garbage†	5.2	4.2	4.1	6.5	1.9	0.381						
Nonfoods‡	8.2	4.6	7.8	13.0	1.4	0.499						

Note: Seasonal values for a food item with a different letter differed statistically ($p < 0.10$).
*Corrected values do not include nonfoods.
†Includes paper, plastic, aluminum foil, and rubber.
‡Includes primarily woody debris and sand.

although ants did not exhibit this relationship (Table 4). Ungulates were also strongly positively related to FN during spring, while small mammals exhibited a similar response during summer and autumn (Table 4).

Discussion

Both contemporary (insect = 18.9%, vertebrate = 10.0%; Table 2) and historic (insect = 40.0%, vertebrate = 7.7%; L.C. Zeigenfuss, United State Geological Survey, 2001 unpublished report) bear diets from RMNP showed the highest uses of animal matter reported for black bears. This was particularly evident when diets were corrected for differential digestibility, as 49.0% of contemporary bear diets consisted of animal matter (Table 2), which increased during summer and autumn when fat accretion in bears is highest (Brody and Pelton 1988). Annual diets of black bears typically consist of ~85% vegetative matter, with the bulk of animal matter coming from insect sources (Hellgren 1993; Pelton 2003). However, relative proportions of vegetative versus animal matter can vary substantially among populations (e.g., southern Yukon: 94.9% vegetative matter and 2.6% animal matter (MacHutchon 1989); northern Wisconsin: 61.7% vegetative matter and 28.0% animal matter (Payne et al. 1998)), of which the highest of these was still less than what was observed in RMNP.

Fecal indices of diet quality reflected logical relationships with foods consumed because higher FN and GE was associated with consumption of animal matter (protein), whereas soft mast and ungulate biomass were associated with higher CF; the former likely owing to the presence of seeds. Fecal indices also indicated relatively high diet quality for bears in RMNP; e.g., crude protein intake was >26%–28%, levels comparable with dietary requirements for omnivores such as domestic dogs (22%–28%; Fraser and Mays 1986) and standard omnivore dietary biscuits used in zoo diets (23%; Fraser and Mays 1986), despite fecal values underestimating true crude protein intake. Patterns in fecal nutrient concentrations also help clarify both overall and seasonal patterns in black bear diets in RMNP. For example, high use of animal matter was likely related to the absence of hard-mast crops, which provide the principal food source for black bears when available (e.g., Hellgren and Vaughan 1988) because of high energy and fat contents (Eagle and Pelton 1983; Inman and Pelton 2002). However, when hard mast is absent, bears compensate by increasing intake of soft mast and animal matter, as these foods can provide substantial sources of energy, fat, and protein (Swenson et al. 1999; Rode and Robbins 2000; Inman and Pelton 2002) that collectively can match or exceed levels attained from hard mast (Kasbohm et al. 1995). Because animal sources are more difficult to find, however, foraging time increases (Rode and Robbins 2000), which may be related to the smaller size of bears typically associated with areas without high density, high abundance food sources (Welch et al. 1997), such as RMNP during the historic period (L.C. Zeigenfuss, United State Geological Survey, 2001 unpublished report).

Seasonal diets also vary geographically depending on foods available. Seasonal use in RMNP appeared to mirror that observed in most other localities that lack hard-mast

Table 3. Comparison of the percent frequency of occurrence (included only the most abundant food item per scat) of food items in scats of black bears (*Ursus americanus*) from Rocky Mountain National Park, Colorado, between historic (1984–1991) and contemporary (2003–2006) periods.

	Grass	Herbaceous	Berries	Insect	Animal
Historic	5.6a	17.5	22.5	44.4a	10.0
Contemporary	31.5b	11.7	18.9	26.1b	11.7

Note: Percent frequencies for a food item with a different letter differed statistically ($p < 0.01$).

Table 4. Results of Pearson's product-moment correlations comparing gross energy (calories/g, where 1 calorie = 4.184 J), crude fat (%), and fecal nitrogen (%) of scats from black bears (*Ursus americanus*) to the percent volume of foods ingested by black bears in Rocky Mountain National Park, Colorado, during spring ($n = 34$), summer ($n = 57$), autumn ($n = 25$), and all seasons combined (annual; $n = 123$), from 2003 to 2006.

		Gross energy			Crude fat			Fecal nitrogen		
Season	Variable	*F*	*p*	*r*	*F*	*p*	*r*	*F*	*p*	*r*
Annual	Grass	**22.2**	**<0.001**	**–0.393**	**6.2**	**0.014**	**–0.220**	**10.7**	**0.001**	**–0.286**
	Herbaceous	**6.1**	**0.015**	**–0.219**	1.6	0.211	–0.114	1.6	0.215	–0.113
	Berries	0.0	0.940	–0.007	**21.8**	**<0.001**	**0.391**	**16.9**	**<0.001**	**–0.350**
	Ants	**11.5**	**0.001**	**0.295**	1.0	0.311	–0.092	0.0	0.931	0.008
	Insects	1.2	0.285	0.097	0.0	0.910	–0.010	**11.9**	**0.001**	**0.299**
	Small mammals	0.0	0.986	0.002	1.4	0.237	–0.107	**18.7**	**<0.001**	**0.366**
	Ungulates	**7.7**	**0.006**	**0.244**	0.7	0.417	0.074	**59.7**	**<0.001**	**0.575**
Spring	Grass	**24.3**	**<0.001**	**–0.657**	**3.7**	**0.064**	**–0.321**	**8.6**	**0.006**	**–0.461**
	Herbaceous	0.0	0.996	–0.001	0.1	0.726	0.062	0.8	0.368	–0.159
	Berries	1.5	0.236	0.209	0.2	0.686	0.072	1.2	0.288	–0.188
	Ants	0.9	0.346	0.167	1.5	0.233	0.210	0.1	0.783	–0.049
	Insects	0.1	0.747	0.058	1.7	0.201	–0.225	**3.1**	**0.088**	**0.297**
	Small mammals									
	Ungulates	**21.0**	**<0.001**	**0.629**	2.6	0.115	0.275	**85.9**	**<0.001**	**0.854**
Summer	Grass	**3.7**	**0.060**	**–0.251**	2.7	0.105	–0.217	**4.2**	**0.047**	**–0.265**
	Herbaceous	**7.7**	**0.008**	**–0.350**	0.3	0.612	–0.069	**3.3**	**0.077**	**–0.236**
	Berries	0.4	0.538	0.083	**8.7**	**0.005**	**0.370**	**5.2**	**0.027**	**–0.293**
	Ants	1.5	0.233	0.161	**6.0**	**0.018**	**–0.313**	0.0	0.861	0.024
	Insects	1.0	0.333	0.131	1.2	0.288	0.143	**15.2**	**<0.001**	**0.465**
	Small mammals	0.3	0.609	–0.069	0.0	0.940	0.010	**22.9**	**<0.001**	**0.542**
	Ungulates	0.9	0.352	0.125	**8.0**	**0.007**	**0.356**	0.3	0.602	0.071
Autumn	Grass	0.1	0.725	–0.074	0.4	0.522	–0.134	0.2	0.669	–0.090
	Herbaceous	**4.6**	**0.043**	**–0.409**	1.7	0.204	–0.263	0.6	0.452	–0.158
	Berries	**3.2**	**0.089**	**–0.347**	**31.7**	**<0.001**	**0.761**	**24.4**	**<0.001**	**–0.717**
	Ants	**11.9**	**0.002**	**0.585**	0.7	0.406	–0.174	1.0	0.325	0.205
	Insects	0.0	0.890	0.029	**3.0**	**0.096**	**–0.340**	**4.0**	**0.059**	**0.383**
	Small mammals	0.2	0.706	0.080	**7.7**	**0.011**	**–0.502**	**13.4**	**0.001**	**0.607**
	Ungulates	0.0	0.897	–0.027	1.2	0.295	0.218	0.1	0.804	–0.052

Note: Significant variables ($p < 0.10$) are in boldface type.

sources (e.g., Raine and Kansas 1990; Kasbohm et al. 1995). Green vegetation (grasses and other herbaceous materials) was the primary food source during spring (Table 2), when actively growing, early phenology plants show seasonal peaks in protein and digestibility (Pritchard and Robbins 1990). Consumption of grasses decreased over time as crude fiber content increased, resulting in lower protein and digestible energy for simple monogastrics such as bears (Pritchard and Robbins 1990). However, even in spring, grasses likely provided little more than minimum requirements for bears in RMNP, as grass consumption was negatively related to GE, FN, and CF in scats (Table 4). Consequently, predation of neonate ungulates and consumption of winter-killed carrion is common during spring for many bear populations (Raine and Kansas 1990; Schwartz and Franzmann 1991) to provide protein to replace muscle mass lost during hibernation. Ungulates provided a greater energy source than green vegetation during spring in RMNP (Table 4) and contributed to the high crude protein levels (>26%) in bear diets; although relatively rare in bear diets in RMNP, ungulate matter had the strongest positive association with FN and GE in spring bear diets, highlighting the importance of ungulates in spring diets even when relatively rare. However, as neonate ungulates age, they become substantially more difficult for bears to capture (Schwartz and Franzmann 1991). As such, presence of ungulates declined

in bear diets, reaching essentially 0 by autumn (Table 2). Consequently, bears increased use of small mammals seasonally, likely to maintain high levels of protein in diets, as consumption of small mammals increased in bear diets from spring to autumn, and small mammals showed the strongest positive association with FN levels in bear diets in autumn (Table 4).

As with many bear populations (e.g., Raine and Kansas 1990; Noyce et al. 1997), ant consumption peaked in summer in RMNP (Table 2). Ants provide an important source of protein, fat, and subsequent energy for bears (Noyce et al. 1997; Swenson et al. 1999). Although results from fecal analyses did not indicate a significant positive relationship between ant consumption and either CF or FN (Table 4), ants were strongly positively related to GE content of bear diets in autumn in RMNP (Table 4). Greater digestibility of alates and pupae may have affected summer results, as these life stages are higher in nutritional value than adults (Auger et al. 2004). Greater assimilation of protein and fats from these sources may yield lower values excreted by bears (Robbins 1993).

While combined use of grasses and other herbaceous foods declined, consumption of berries and hard mast increased from spring through autumn (Table 2). Soft mast is typically high in energy content but low in protein (Rode and Robbins 2000), while we observed the strongest relationship between berry consumption and fecal CF in both summer and autumn (Table 4). These results were likely influenced by the indigestibility of seeds. Most of the energy associated with berry consumption is in the form of simple sugars (Rode and Robbins 2000); these are readily utilized by bears leaving primarily the indigestible seeds and casings to be excreted. Seeds are typically high in fat (Robbins 1993) and likely accounted for the high values that we observed. This potentially minimized effects of other foods on CF, thus resulting in weak and often counterintuitive models of CF (Table 4), although foods other than ungulates used by bears in RMNP are also typically low in CF (Pritchard and Robbins 1990). Additionally, while Brody and Pelton (1988) suggested that protein assimilation by bears declines in autumn, we did not observe any seasonal differences in FN even though diets varied across seasons (Table 2), indicating that bears were able to achieve high and relatively constant protein levels in their diets, similar to other large omnivores such as baboons (Codron et al. 2006). This result suggests that bears were able to maintain or increase protein consumption annually in RMNP; lacking hard mast, high use of animal matter may be critical to accrual of fat levels for hibernation in RMNP. If protein was assimilated less in autumn, FN levels should have risen in RMNP to reflect increasing use of animal matter, rather than remaining similar.

The most notable difference between historic and contemporary diets of bears in RMNP was increased use of anthropogenic foods, with annual intake 15.2 times more common in the contemporary period. Increased use of human foods may be reflected in body condition of bears (mean body mass of females: historic = 52 kg, contemporary = 59 kg; mean body fat of females: historic = 15.0%, contemporary = 24%; Baldwin and Bender 2009), as anthropogenic foods yield higher caloric, protein, and fat intake than most natural diets (Stringham 1989). Furthermore, use of human-use areas by bears was positively related to bear condition in RMNP (Baldwin 2008). Comparisons of the frequency of occurrence of natural food items between historic and contemporary periods also suggested that diets were of higher quality historically (i.e., less grass, more insects; Table 3). Supplementation of anthropogenic foods into bear diets was likely required to attain the size and condition seen in the contemporary bear population in RMNP.

Increased use of human foods can result in negative encounters with humans (Tate and Pelton 1983; Peirce and Van Daele 2006). Historically, bears in RMNP were believed to avoid human-use areas (McCutchen 1990). However, development along the boundary of RMNP has increased the potential for human–bear encounters (L.C. Zeigenfuss, United State Geological Survey, 2001 unpublished report), and bears in the contemporary population no longer avoid human-use areas (Baldwin 2008). Although current use of anthropogenic foods (5.2% of fecal volume annually) are not as high as some other populations (Yosemite National Park, California: 15% by volume (Graber and White 1983); San Gabriel Mountains, California: 33% by volume (Stubblefield 1993)), the trend of increased use parallels that observed in the Lake Tahoe region of Nevada (Beckmann and Berger 2003*a*, 2003*b*), which ultimately led to emigration of most bears out of wildland areas.

Management implications

Bears in RMNP heavily used grasses and other herbaceous plants during spring and early summer, but nutritional gains from these resources were low compared with animal matter. Conversely, vertebrate consumption made up <12% of bear diets annually in RMNP, yet provided a valuable source of protein, fat, and energy for the population. Maximizing foods high in energy, protein, and fat benefits bears, but is difficult given the high elevation of RMNP and the Park's "natural regulation" philosophy. Because plant material is much more abundant, enhancing nutritional quality of these herbaceous foods is important in RMNP to encourage bears to use natural foods rather than anthropogenic alternatives. Because most use of grasses occur in spring, prescribed burning and letting wildfires burn to the extent possible could provide high-quality early successional habitats, increased forage biomass, more rapid green-up, and increase nutritional quality of foods because of decreased canopy cover, released nitrogen from ground litter, and warming of microclimate (Neary et al. 1999). Additionally, dead and down ground cover (i.e., fallen logs from dead trees) could increase after fires, providing abundant logs and cover for ants, other insects, and small mammals (Noyce et al. 1997; Suzuki and Hayes 2003).

RMNP has proposed several alternatives for reducing elk numbers in RMNP (National Park Service, 2006 unpublished report). Such a reduction would reduce available ungulate biomass owing to loss of winter-killed carrion and potentially fewer neonates. Such actions warrant careful consideration and future monitoring given the importance of ungulates as a protein and energy source in spring diets. If insufficient ungulate biomass is available, bears may compensate by switching to other high protein – high energy foods, particularly increased use of anthropogenic foods. We have documented a shift in bear use away from wild-

lands into human–wildland interface areas (Baldwin 2008, Baldwin and Bender 2008). This shift, combined with increased use of anthropogenic foods over the last 15–20 years, warrants further monitoring given the propensity of bear populations to habituate to urban settings (Beckmann and Berger 2003*a*, 2003*b*), frequently resulting in conflicts detrimental to local bear populations. While increased use of anthropogenic foods has likely contributed to increased size, condition, and productivity of bears in RMNP (Baldwin and Bender 2009), these effects could be offset by future bear–human conflicts presenting a problematic management challenge.

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