Nutritional ecology of ursids: a review of newer methods and management implications

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Abstract: The capability to understand the nutritional ecology of free-ranging bears has increased dramatically in the last 20 years. Advancements have occurred because (1) managers and biologists recognized the need to link habitat quality, productivity, and variability with bear movements, home ranges, and demographic parameters like reproductive output, survival, and population growth, and (2) several research teams are using new methods to build on the results of earlier field studies. Our ability to couple new field methods and empirical field research with controlled experiments using captive bears has been central to our increased understanding of bear nutrition. Newer methods include the use of stable isotopes to quantify assimilated diet and nutrient flows within ecosystems, bioelectrical impedance to measure body composition, and naturally occurring mercury to estimate fish intake. Controlled experiments using captive bears have been integral to developing methods, isolating specific variables by controlling the environment, and providing additional nutritional understanding necessary to interpret field observations. We review new methods and apply our increased understanding of bear nutritional ecology to 3 management issues: (1) the importance of salmon (*Oncorhynchus* spp.) to brown bears (*Ursus arctos*) in the Pacific Northwest, (2) the consequences of the closure of the Yellowstone garbage dumps to grizzly bears, and (3) the relocation of problem bears.

Key words: American black bear, foraging, grizzly bear, mercury, nutrition, stable isotopes, *Ursus americanus*, *Ursus arctos*, Yellowstone

Bears are an enigmatic family. Morphologically and taxonomically, they possess all the traits of carnivores but, with the exception of the polar bear (*Ursus maritimus*), have diets often comprised primarily of plant matter. Many of the bear species evolved with a generalist omnivore strategy that allows them to successfully occupy a broad array of the world's biomes. Today, all bear species have declined in numbers and distribution due to effects of human activities (Servheen et al. 1999). Understanding the nutritional ecology of the 8 bear species is of interest from a purely theoretical perspective but is also important when we are faced with worldwide issues of conservation. We cannot plan, implement, and successfully manage conservation programs without a broad base of solid biological knowledge.

Nutritional information in many bear ecology studies has been limited to using body weights as indices of body condition or fat content, uncorrected fecal residues as indices of food habits, and food abundances and gross energy or crude protein content as indices of nutritional value (Rogers 1976, Elowe and Dodge 1989, Stringham 1990, Mattson et al. 1991). While these are important measures and starting points for any nutritional ecology study, the nutritional ecologist would like to actually measure food intake, changes in fat and lean body mass, foraging efficiencies and rates of gain, and the amounts of digestible energy or protein coming from the various foods to directly relate bear productivity or habitat quality to food characteristics (Atkinson and Ramsay 1995, Hilderbrand et al. 1999*a*).

Our understanding of the nutritional ecology of bears has advanced significantly during the past 20 years. Several reasons for this advancement are the knowledge and insight provided by earlier field ecology studies,

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involvement of several teams of investigators, development of new field methods, the combining of empirical field research with controlled experiments using captive bears, and the recognition that nutritional ecology is key to understanding ecosystem processes and providing guidance to managers. To illustrate several of these points, we will discuss (1) several of the newer methods, and (2) both historical and current management issues for which an understanding of nutritional ecology can provide significant insight.

Newer methods in nutritional ecology

Nutritional understanding of any wild species will always be very limited without the use of captive animals for controlled studies. Prior to 1986 when the Washington State University Bear Research, Education, and Conservation Program was established, nutritional studies on wild bears were largely limited to food habits and the development of broad ecological relationships between inter-annual cycles of food production and bear productivity (Rogers 1976, Elowe and Dodge 1989); research on captive bears was limited to quantifying digestive efficiency and the physiology of hibernation (Nelson 1973, Watts et al. 1981, Dierenfeld et al. 1982, Bunnell and Hamilton 1983, Watts et al. 1987, Hellgren 1998). Indeed, our early studies with captive bears were along these same lines of investigation (Pritchard and Robbins 1990, Farley and Robbins 1995). However, in time we recognized that the greatest conservation value for studies of captive bears was to augment field ecology studies, either by developing new techniques (Farley and Robbins 1994; Hilderbrand et al. 1996, 1998; Felicetti et al. 2003*a*, 2004) or providing critical information that could not be measured on free-ranging bears (Farley and Robbins 1995; Welch et al. 1997; Rode et al. 2001; Felicetti et al. 2003*a*, 2004). It is the synergism between studies on captive bears and wild bears that leads to the greatest understanding of the nutritional ecology of wild bears (Hilderbrand et al. 1999*a*,*b*,c; Felicetti et al. 2003*a*, 2004). Below, we provide several examples.

Estimating assimilated diet: stable isotopes

Early field naturalists (e.g., Murie 1981) and more recent wildlife biologists (e.g., Mattson et al. 1991, McLellan and Hovey 1995) relied heavily on fecal analysis to quantify diets for various bear species. Such research advanced our knowledge about the generalist omnivore nature of both grizzly bears and American black bears. Early predator–prey studies, particularly in Alaska (e.g., Franzmann and Schwartz 1986, Ballard and Miller 1990, Gasaway et al. 1992), revealed the predatory nature of both grizzly and American black bears (*Ursus americanus*) and dispelled the commonly held belief that meat consumption in bears was primarily scavenged carrion (Seton 1929, Bradt 1946, Chatelain 1950, Erickson 1965, Juniper 1978). Results of this work suggested that bears were quite efficient predators in spite of fecal examination that suggested a diet composed primarily of plant matter. Such discrepancies between known predation rates and fecal analysis led us to investigate the differential digestibility of meat and plant matter by bears.

Our work (Pritchard and Robbins 1990, Hewitt and Robbins 1996) was instrumental in illustrating how the differential disappearance of foods during digestion and passage changed the ratios between the foods consumed and the residues excreted. This work clearly showed that the ratio of items identified in scat was not the same as the proportion consumed. Plants, particularly in later stages of growth, were poorly digested and readily identified in the feces when compared to meat from ungulates or fish. We developed correction factors to improve our ability to estimate diet constituents, but such corrections are subject to error depending on the volume of identifiable, nondigestible animal remains that are consumed. For example, the correction factor for meat can vary 2–fold depending on the ratio of meat to hair that is consumed (Schwartz and Franzmann 1991:36, Hewitt and Robbins 1996). Clearly, additional work was needed to improve our ability to determine the importance of different foods.

The use of naturally occurring stable isotopes of carbon, nitrogen, and sulfur to estimate assimilated diet has been the single greatest breakthrough in the nutritional ecology field during the past 20 years. Stable isotopes are non-radioactive atoms that contain an extra neutron and occur in parts per thousand (‰) relative to the more common form of that element. Isotope concentrations are measured using isotope ratio mass spectrometers (IRMS), which count the number of isotopes of a particular element that pass by an electromagnet and are differentially deflected based on their mass. Because an element has to form a gas to be analyzed, the analysis is limited to carbon (C), nitrogen (N), sulfur (S), hydrogen (H), and oxygen (O). However, because the analysis requires ≤2 mg of organic matter, hair snares or other means for collecting very small samples can provide an adequate sample for isotope analyses. Thus, the same hair samples collected for non-invasive genetic sampling to monitor population size, habitat use, or movement patterns of bears can also be used to estimate their assimilated diet.

Because stable isotope ratios change as they move from plants through a series of consumers, isotope analyses of blood or hair can be used to determine the percent of C, N, or S within the bear that came from plants or animals. The plant or animal components of the diet can be further subdivided when specific items have unique isotope signatures. For example, the nutritional importance of whitebark pine nuts (*Pinus albicaulis*) to the grizzly bears of Yellowstone has been estimated using sulfur isotopes as pine nuts, with a sulfur signature of 9.2 ‰ (SD = 1.3), differed significantly from all other plants (1.9‰, SD = 1.7) and animals (1.3‰, SD = 2.2 for army cutworm moths (*Euxoa auxiliaris*) to 3.1‰, SD = 2.6 for ungulates) (Felicetti et al. 2003*a*). Meat consumed by bears feeding on a mixture of marine (e.g., salmon to seals) and terrestrial animals (e.g., insects to ungulates) also can be proportioned because marine animals frequently have significantly higher ^{13}C and ^{15}N isotope signatures than terrestrial animals. The differing carbon signatures reflect differing sources (atmospheric carbon dioxide versus soluble bicarbonate) and long-term geological processes in the terrestrial and marine environments, whereas the higher nitrogen signatures of many marine foods are due to more trophic levels in marine systems than in the terrestrial and, therefore, increased enrichment at the top marine trophic levels (Hilderbrand et al. 1996, Felicetti et al. 2003*b*).

The cost of isotope analyses has decreased and speed has increased as IRMS have become more common, sensitive, and automated. Currently, carbon and nitrogen isotope analyses cost ~US$10/sample (2004), can be done simultaneously on the same sample, and generally take only a few days. Sulfur analyses are more complex and therefore more expensive (~US$30/sample). Similarly, blood and hair samples taken from a single bear when captured can provide several temporal estimates of assimilated diet. For example, plasma samples can provide assimilated diet estimates during the past week, red blood cells during the past 3 months, hair during the past year (if the hair is old) or since it began growing (if new hair), and bone during several years to a lifetime (Hilderbrand et al. 1996). If the growth characteristics of fully-grown hair have been measured, hair can be sectioned and the parts used to estimate seasonal diets.

Although care in sample collection and analyses are critical, equally important is the selection of the model used to estimate assimilated diet. When working with bears feeding only on terrestrial foods in which a plant–animal dietary division is sought and therefore ^{15}N is the only important variable, a simple linear regression or ratio can be used (Hilderbrand et al. 1996). However,

when bears consume foods in which 2 isotopes are measured, that is, a mixture of marine and terrestrial foods in which ^{13}C, ^{34}S, or ^{15}N are measured, the correct model must simultaneously estimate the best solution for 2 isotopes within a 2-dimensional space (Felicetti et al. 2003*b*, Phillips and Gregg 2003).

The use of stable isotopes to understand diet allows bear researchers to look at the importance of different foods to different age and sex classes through time. This has not been possible with fecal analyses. For example, we and others have compared the assimilated diets of ancestral bears dating back thousands of years to modern day bears by using samples from skeletons or pelts housed in museums (Bocherens et al. 1994, Matheus 1995, Hilderbrand et al. 1996, Jacoby et al. 1999). Stable isotopes also have been used to determine that male grizzly bears are more carnivorous than females (Jacoby et al. 1999, Hobson et al. 2000), that grizzly bears and black bears utilize salmon to a different extent depending on whether they are sympatric or allopatric (Jacoby et al. 1999), and that grizzly bear populations that gain most of their nutrients from plant matter have smaller individuals at much lower density than populations that feed on abundant salmon (Hilderbrand et al.1999*c*). While several of these observations have corroborated earlier conclusions based on more traditional field techniques, the use of stable isotopes can frequently lessen the time and therefore cost of such measurements.

Additionally, the use of isotopes to estimate assimilated diet coupled with DNA identification of individual females will lead to a better understanding of the interactions between the use of specific food resources and reproductive performance within an ecosystem. Although this has been done at the population level (Stringham 1990, McLellan 1994, Hilderbrand et al. 1999*c*), such analyses have not been conducted for individuals within a population. Such studies can provide insight into the possible consequences of changing food resources within an ecosystem that might occur naturally or as a consequence of human activity (i.e., over-harvest of salmon, introduction of exotic pathogens, or global climate change) and help explain the variability observed among individuals.

Stable isotopes, as commonly used, do not estimate diet in the sense of specific food habits. Stable isotopes estimate assimilated diet, or the relative sources of carbon, nitrogen, or sulfur that are retained in the tissues of the animal. Because of differing digestibility and metabolism of foods, bears in populations with access to abundant meat (e.g., salmon or large ungulates) can have

Table 1. The differences between food habits, fecal volume, and assimilated diets for grizzly bears. Fecal volume was estimated by sorting the contents of feces collected in the field, food habits was estimated from fecal volume by correcting for differential disappearance, and assimilated diet was estimated by multiplying the concentration of energy and protein in each food by its digestibility (adapted from Pritchard and Robbins 1990, Hewitt and Robbins 1996, Rode et al. 2001).

Diet item	Food habits (% diet dry matter)	Fecal volume (%)	Assimilated diet (% energy)	Assimilated diet (% protein)
Ungulates	54	31	66	48
Rodents	9	4	7	11
Trout	23	1	22	34
Insects	2	3	1	2
Animal matter	88	38	96	95
Grasses and sedges[a]	6	48	1	2
Forbs	1	5	>1	>1
Roots	3	5	1	>1
Fleshy fruits	1	2	>1	>1
Pine nuts	1	2	>1	>1
Plant matter	12	62	4	5

[a] *Carex* spp.

fecal residues that are heavily weighted toward vegetation, food habits that are less dominated by plants, and assimilated diets that are heavily weighted toward animal matter (Table 1). Thus, any discussion of 'diet' must be carefully evaluated relative to the methods used. For most nutritional ecology studies, the important variable is the energy, nitrogen, or sulfur contribution from the various dietary constituents to the overall nutritional status of the individual (i.e., assimilated diet). For many predator–prey studies examining the number or amount of prey consumed and perhaps the effect on prey populations, the important variables are food habits and the mass or number of each prey species consumed. Both assimilated diet and food habits can be estimated from stable isotope analyses, but the estimates require different information and models (Phillips 2001, Koch and Phillips 2002, Robbins et al. 2002, Phillips and Gregg 2003). However, all stable isotope methods and models estimate only the relative dietary proportions and do not estimate absolute amounts of food consumed.

Estimating marine or freshwater fish intake with naturally occurring mercury

One of the most important needs in many nutritional ecology studies is to estimate absolute intake of specific foods. For example, fisheries managers considering the needs of wildlife when setting salmon escapement goals need to know how many pre-spawn salmon should be allotted to bears, otters (*Lontra canadensis*), and other wildlife. Historically, there have been few opportunities to quantify long-term food intake by wild bears. One of the very few methods has been close observations of habituated bears (Rogers and Wilker 1990), although the personnel and time required to habituate bears and collect long-term, continuous data can exceed the resources of most bear research programs. In special circumstances (such as McNeil River in Alaska), observers can count salmon caught by individual bears. But even these studies are limited because investigators usually can not quantify salmon intake at night or when a specific bear leaves the observation area. Similarly, when multiple bears fight over a given fish and consume unknown amounts or when dominance hierarchies relegate subordinate bears to less observable or more distant areas, the difficulty of understanding salmon intake on the limited budgets characteristic of wildlife studies becomes insurmountable.

Hilderbrand et al. (1999a) circumvented these problems by first measuring the amount of salmon necessary to produce specific rates of gain in captive bears. They then applied those levels of fish intake to wild bears whose rate of weight gain was determined by capturing and weighing bears at the beginning and end of the salmon-feeding season and whose assimilated diet had been estimated by stable isotope analyses. This method did not require observation of individual bears, a large number of observers, or direct measure of fish consumption. However, estimated intake using this method must be viewed as a minimum because wild bears are likely more active than captive bears, and the increased activity elevates the maintenance requirement and decreases the rate of gain per unit of salmon intake. This approach also requires multiple captures and radiotelemetry to track individuals. Because bears in many populations may not be caught at all (such as populations in National Parks that require non-intrusive research) or can not be caught

at the critical periods necessary to measure weight change (e.g., many forested environments), other less intrusive methods are needed to estimate intake.

Mercury and other heavy metals are frequently bioaccumulated in aquatic ecosystems (Ben-David et al. 2001). For example, while most bear foods in terrestrial ecosystems contain ≤6 ppb mercury, salmon returning to hatcheries in Idaho contain 240 ppb mercury and spawning cutthroat trout (*Oncorhynchus clarki*) from Yellowstone Lake contain 508 ppb (SD = 93) mercury in their dry matter (Felicetti et al. 2004). Because mercury is deposited in growing hair in proportion to its intake, hair contains a record of the amount of mercury and, therefore, fish that has been consumed. By combining captive bear feeding trials to quantify the relationship between fish–mercury intake and hair mercury content, hair snares to collect hair samples from wild bears, and DNA analyses to identify the gender and identity of each wild bear, Felicetti et al. (2004) estimated the amount of cutthroat trout consumed by individual grizzly bears in the Yellowstone Lake area. They concluded that males consumed 92% of all cutthroat trout and that grizzly bears consumed <0.2% of the spawning population. In contrast to Hilderbrand et al.'s (1999*a*) approach, the mercury technique did not require the capture of even one wild bear and would not be affected by the potentially differing activity levels between captive and wild bears. However, far greater understanding of the temporal characteristics of hair growth and factors affecting hair composition in wild bears are needed before the value of this and other hair-based techniques can be determined.

Estimating body composition: bioelectrical impedance analysis (BIA) and dual energy X-ray absorptiometry (DEXA)

Wildlife biologists have long wanted to quantify body composition as an index or predictor of animal well being, productivity, diet quality, or habitat carrying capacity. The focus by nutritional ecologists on measuring body composition or condition rather than relying only on body weight occurs because (1) bears have tremendous plasticity in altering the composition of the weight gain and therefore the amount of fat at a given body weight (Felicetti et al. 2003*a*), and (2) body weight, while generally correlated to body fat content, is confounded by differing skeletal sizes (Noyce and Garshelis 1994, Atkinson and Ramsay 1995, Samson and Huot 1995, Cattet et al. 2002).

Historically, methods to estimate body composition have been very crude (e.g., body weight, kidney fat

index, or condition scores), very destructive (e.g., kill and grind), or too technical and time-consuming for most field studies (e.g., water dilution) (Farley and Robbins 1994). Two newer methods that eliminate some of these problems have been used successfully on both wild and captive bears (Farley and Robbins 1994; Hilderbrand et al. 1998, 1999*a*; Harlow et al. 2002; Noyce et al. 2002; Felicetti et al. 2003*a*). The first is a field-appropriate technique called bioelectrical impedance analysis (BIA). A machine, which is about the size of a cell phone, measures the resistance to the flow of a small electrical current as it passes through the body. Resistance is directly proportional to body fat content and thus provides a fairly accurate measure of body composition once calibrated for the particular species. The procedure takes approximately 5 minutes, requires an accurate measurement of the bear's body weight, cannot be used on injured, dehydrated, or dead bears, and requires significant investigator training and standardization of measurement techniques. The second method (DEXA), while more accurate than BIA, can only be used on captive bears as the machine is room-sized. However, both these techniques indicate that with future developments and miniaturization of the electronics, body composition of bears will be measured routinely, accurately, and comparably between studies under field conditions.

Population and management implications of nutritional ecology studies
The importance of healthy salmon populations to bears

The most complete bear nutritional ecology story to emerge in recent years has been that of salmon, grizzly bears, and ecosystem functioning. Enormous pressures are being placed on salmon and their aquatic habitats by commercial and sport-fishermen, eco-tourists, developers, farmers, ranchers, loggers, miners, and other extractive or water-using industries. Some individuals associated with these special interest groups have erroneously assumed that the high-density, large-bodied bears that consume salmon can simply shift their diets away from salmon to berries and vegetation so spawning salmon or the rivers can be used for other purposes. Miller et al. (1997), Welch et al. (1997), Hilderbrand et al. (1996, 1999*a*,*c*), and Rode et al. (2001) demonstrated that abundant, easily acquired meat sources, such as large salmon runs, are an obligate food resource for large, high-density

brown bears. Although brown bear populations exist without salmon, individuals in these populations are smaller, reproduce less often, and exist at densities 1/50th of those occurring in salmon-feeding populations (Miller et al. 1997). Similarly, brown bears are an integral link in conveying marine-derived nutrients from salmon into riparian and terrestrial communities (Hilderbrand et al. 1999*b*; Helfield and Naiman 2001, 2002; Drake et al. 2002). On average, 20% of the nitrogen in riparian conifers along major salmon-spawning streams in Alaska came from salmon, and 80% of that nitrogen passed through brown bears. Thus, future management of salmon can no longer be the sole province of fisheries managers, and escapement goals for spawning salmon streams must place a much greater emphasis on the nutrient needs of the entire freshwater and terrestrial ecosystems (Hilderbrand et al. 2004).

A nutritional understanding of the closure of Yellowstone garbage dumps

A very similar analogy with similar consequences occurred when garbage dumps were closed between 1968 and 1970 in Yellowstone National Park (Craighead et al. 1995). Food residues in the dumps provided a valuable resource for many of Yellowstone's grizzly bears. At the Trout Creek dump, 129,000 liters per day of edible and inedible garbage was dumped during the 1960s. Thus, all age and sex classes of grizzly bears used the dumps. Once the decision was made to close the dumps and return the bear population to natural foods consistent with Park Service policy, much of the acrimonious debate that followed focused on whether the dumps should be gradually phased out or closed suddenly. Unfortunately, we now recognize that much of that debate was misplaced because of a lack of understanding of bear nutritional ecology.

Virtually all of the elevated grizzly bear mortality occurred within 2 years of dump closure and was confined to adults (Craighead et al. 1995:430) ($F = 20.24$, $P < 0.0001$; ANOVA and least square means, SAS Institute Inc. 1998). There was no significant change in the observed mortality of cubs, yearlings, or 2–4 year-old subadults. Average adult male weight during the years of abundant garbage was 336 kg in the fall as compared to 180 kg after dump closure (Craighead et al. 1995). These large males accounted for 57% of the increased adult mortality in the 2 years following dump closure. Their removal was probably unavoidable irrespective of the timeline for dump closure, as they had grown to a skeletal and lean body mass size that could not be supported by poorer quality, more dispersed, and

more difficult to acquire natural foods. For example, adult males currently in the Greater Yellowstone Ecosystem have a fall body fat content that averages 28.8% ($n = 6$, range of 19–35) (Schwartz, unpublished). For the adult males that fed at garbage dumps to have reverted to natural foods and quantitatively conserved lean body mass, but retained body fat content equal to that in current males would require that the garbage-fed males had to initially average 62% body fat, a level that exceeds that found in salmon-feeding brown bears, captive grizzly bears, and obese polar bears (Farley and Robbins 1994, Atkinson and Ramsay 1995, Hilderbrand et al. 1998, 1999*a*).

The size of adult females, 171 kg prior to and 132 kg after dump closure, might have been closer to what could be supported by natural foods, but even that assumption may be doubtful because the weight differential probably represents more than surplus body fat. For example, adult females currently in the Greater Yellowstone Ecosystem have a fall body fat content of 27.8% ($n = 5$, range 24–33%) (Schwartz, unpublished). For adult females feeding at the garbage dumps to have reverted to natural foods and quantitatively conserved lean body mass, but retained body fat content equal to that in current females would require that the garbage-fed females had to initially average 44% body fat, a level that approaches the highest levels found in salmon-feeding brown bears (Hilderbrand et al. 1999*a*) and captive grizzly bears (Farley and Robbins 1994, Hilderbrand et al. 1998) that are much heavier.

The body size of an individual bear determines and is determined by the food resources the individual bear exploits. For most naturally occurring foods, optimum bear size is determined by the rate at which the food can be harvested and assimilated and its nutritive value relative to the absolute requirements of the individual. With bears, our research shows that this leads to a series of bell-shaped curves between animal body weight and the maximum rate of gain that can be achieved on a particular food (Welch et al. 1997, Rode et al. 2001). For bears feeding on berries or vegetation, optimum body mass ranges between 80 and 150 kg (Fig. 1, 2), which encompasses the mean adult female mass in numerous grizzly bear and black bear populations that feed primarily on plant matter, as well as the size of adult male and female spectacled bears (*Tremarctos ornatos*) and giant pandas (*Ailuropoda melanoleuca*), two other primarily herbivorous bears (Schaller et al. 1985, Brown 1993, Welch et al. 1997, Hilderbrand et al. 1999*c*).

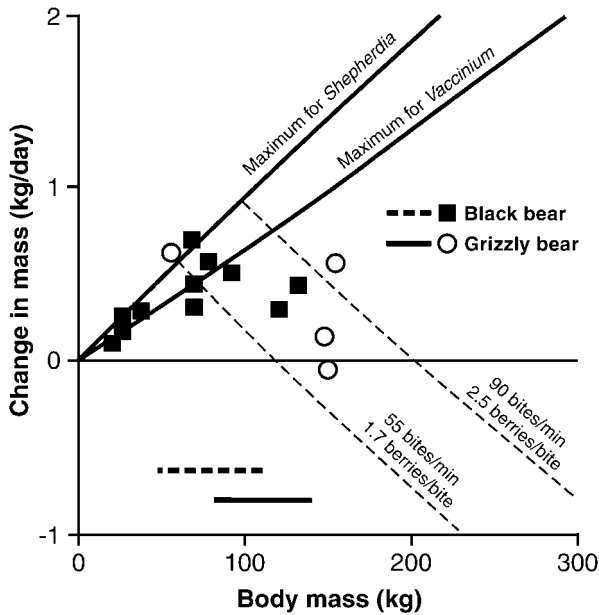The optimum-sized bear feeding on berries is determined by rate of intake, because most preferred

Fig. 1. Theoretical maximum and observed gains in body mass by wild black and grizzly bears consuming huckleberries (*Vaccinium membranaceum*) and soapberries (*Shepherdia canadensis*). The solid dark lines are for bears that are not limited by rate of intake. The dashed lines are predicted mass changes imposed when daily feeding time is limited to 12 hr/day for specified bite rates and bite sizes. The maximum rate of gain occurs for bears weighing about 100 kg, and the average adult female size in black bear and grizzly bear populations that feed primarily on berries in the fall (solid horizontal bars) are consistent with the weight range over which maximum gain occurs. Reprinted with permission from Welch et al. (1997).
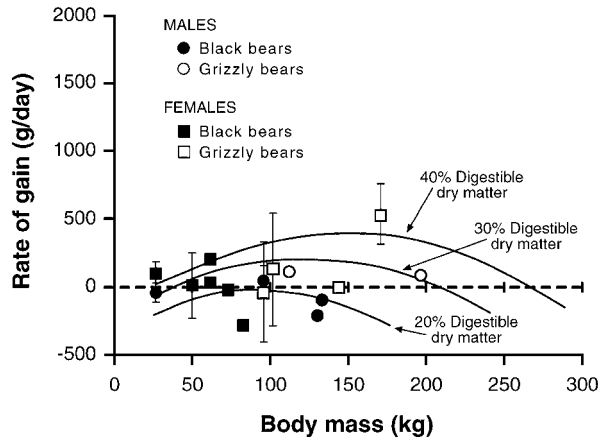

Fig. 2. Observed rates of weight gain (data points) for wild grizzly bears and black bears feeding on plant and animal matter during the spring and summer before significant salmon or berry consumption (Jonkel and Cowan 1971, Blanchard 1987, Hellgren et al. 1989, Noyce and Garshelis 1998, Hilderbrand et al. 1999*b*). The lines are rates of gain observed (40% digestible dry matter) or predicted (30% and 20%) by captive grizzly bears consuming vegetation at 3 levels of digestibility (adapted from Rode et al. 2001). As dietary quality decreases from 40% dry matter digestibility to 20%, the optimal bear size where gain is maximized moves from as much as 200 kg to 100 kg.

berries are highly digestible but relatively small. In contrast, the determinant of size for bears that feed on vegetation tends to be food digestibility and subsequently selectivity, because nutritional quality of most vegetation is much lower than berries. Although meat in the form of ungulates, cutthroat trout, and army cutworm moths is seasonally available and provides the basis for larger bears in Yellowstone than in purely herbivorous populations (Hilderbrand et al. 1999*c*, Jacoby et al. 1999), plant matter is the staple during either some seasons or some years for all Yellowstone grizzly bears (Mattson et al. 1991, Felicetti et al. 2003*a*). Therefore, we suggest that the only nutritional options for the large, garbage-fed adult males and females were to starve, move into developed areas and seek anthropogenic food suitable to support their body size and, thereby, be killed

as problem bears, or learn to hunt wild ungulates. Carnivory is one of the few foraging strategies that enables bears to grow very large (Hilderbrand et al. 1999*c*), but we doubt if the requisite hunting efficiency for wild ungulates could have been achieved by the excessively large, garbage-fed bears in virtually any time frame. Learning to use other, lower quality food resources if dumps had been closed gradually was not an energetic option for these large-bodied bears and would have only delayed their ultimate fate once all garbage dumping had ceased.

Finally, an assumption inherent to the arguments for a gradual closure of the dumps was that bears would share a more limited supply of garbage such that gradual weaning of all bears would have occurred. Our experience with both wild and captive grizzly bears consuming high-quality, defendable, but limited food resources that can be exploited risk-free relative to humans is that food sharing by dominant bears does not occur. Aggression by larger, dominant bears would have forced more subordinate bears away from the dumps as the amount of garbage declined below what was necessary to meet the needs of the more dominant

bears. Thus, even gradual closure of the dumps would have had the same effect of suddenly weaning individual bears based on their position in the dominance hierarchy and, as the Park Service argued, would have only prolonged the management problems.

Thus, if natural (spawning salmon) or human-created ecocenters (garbage or livestock dumps) are used long-term by bears such that they become more numerous and larger in body size than can be supported by other natural foods, managers need to recognize the inevitable problem bear consequences of loss or removal of these food sources. Management-created ecocenters may be helpful in recovering populations in the short-term by improving bear condition and thereby increasing reproductive output and survival while reducing movements and bear–human conflicts, but they pose economic costs if they are maintained long-term and risks to both bears and people if they are ultimately removed. Creating and closing of such ecocenters requires a great deal more insight into the nutritional ecology of bears than has been exhibited in previous discussions. For example, if ecocenters are to be created in areas where meat resources will always be limited, vegetation, such as monotypic stands of white clover (*Trifolium repens giganteum*) that provides relatively large, nutritious bites (Rode et al. 2001), or grain crops could be planted and would, perhaps, hold bears away from developed areas while providing nourishment more similar to that used by the size of bear that natural foods would ultimately support.

Re-evaluation of relocation of some problem grizzly bears

Bears that conflict with humans are often transported to more remote environments with the hope that they will remain in wild habitats and stay problem-free. However, transporting a bear is often a short-term solution as high rates of return are common (Judd and Knight 1980, Miller and Ballard 1982, Blanchard and Knight 1995). Conflicts and confrontations between bears and humans arise because of a number of reasons, including food conditioning, property damage, livestock or crop depredation, and aggressive encounters; but they are typically associated with either food or defense. Most occur during the summer or fall season, particularly in poor food years, when bears are hyperphagic (Mattson et al. 1992, Blanchard and Knight 1995). Many problem bears in natural ecosystems (e.g., Greater Yellowstone Ecosystem) that do not have access to anthropogenic foods are nutritionally stressed and in poor physical condition (Blanchard and Knight 1995, Schwartz et al. 2002). Survival rates of these problem

bears are typically low (Mattson et al. 1992, Riley et al. 1994, Blanchard and Knight 1995) and can represent a sink to an otherwise healthy population (C.C. Schwartz, unpublished data; M.A. Haroldson et al. Interagency Grizzly Bear Study Team, Northern Rocky Mountain Science Center, Montana State University, Bozeman, Montana, USA, unpublished data).

Relocation of problem bears is frequently conducted with minimal consideration for the quantitative aspects of their nutritional ecology. Bears are intelligent animals and learn the physical locations and seasonal availability of food resources within their home range. Removal of such animals from familiar home range and relocation into unfamiliar habitat immediately imposes additional stress on an already nutritionally compromised individual. Presumably, resident bears occur at the relocation site and will dominate a new bear with no prior knowledge of the area and the distribution of available foods.

Similarly, there may be little opportunity to match the food resources in the new relocation area to the absolute requirements of a specific bear. This may be a particular problem in relocating large adult males and females. For example, livestock-eating bears from east of the Continental Divide in northern Montana are frequently moved into the less developed North Fork ecosystem west of the Continental Divide, where available foods are diverse but consist primarily of berries and vegetation (Riley et al. 1994, McLellan and Hovey 1995, Hilderbrand et al. 1999*c*, Jacoby et al. 1999, Manley 2003). Many of the East Front bears never get into trouble as they feed on carcasses of cows dying from a multitude of other causes. However, the abundant, high quality food available in livestock boneyards can create exceptionally large adult bears. For example, a 318 kg male that became a problem bear when it killed a cow in 2002 was relocated from the East Front to the North Fork (Manley 2003). As discussed previously, such a bear is very unlikely to meet its nutritional needs on a dispersed, lower quality, plant-based diet. Indeed, this bear returned to its original home range on the East Front within 10 days. Similarly, 80 to 90% of such relocated bears that are moved from the East Front to the North Fork return to their former home ranges (Manley 2003). Nutritionally, such outcomes should be expected. Thus, we suggest that the relocation of problem bears be treated as a research opportunity in which the causes of success or failure should be analyzed in an ecological context.

For particularly important individuals (i.e., adult females) in threatened or endangered populations that

become problem bears only during a year of food scarcity, we suggest that a new approach might be considered to conserve these highly valued individuals. For example, rather than translocating an already nutritionally stressed bear into unfamiliar habitat with the hope that it will survive and not return to a conflict site, it might be more useful to temporarily provide food within its existing home range to remove the food-based conflict, to improve the animal's nutritional state, and to keep it alive until the natural food crisis passes. Such supplemental feeding must be done in a way that prevents the bear from associating the supplemental food with humans. Supplemental feeding of large numbers of wild black bears already occurs in the Pacific Northwest and is successful at reducing conifer damage during the early spring when other food resources are limited (Partridge et al. 2001, Ziegltrum and Nolte 2001). Similarly, aversive-conditioning to frighten away problem bears might be much more successful if combined with an understanding of the nutritional status of the individual bear and the cost:benefit to that particular bear of leaving a specific food resource.

Future research needs

Understanding the nutritional ecology of bears is an enormously challenging area of investigation. As in the past, the field needs to advance on a broad front supported by studies of both captive and wild bears. Future research could include understanding the energetic and productivity cost sustained by bears due to human disturbance and displacement, further refining stable isotope methodology and models, further refining body composition measures, and understanding the value of specific foods within ecosystems to bear productivity such that the effects of environmental change can be predicted. Bears and their management will be the ultimate beneficiaries of this new knowledge.

Acknowledgments

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