The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears

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Abstract: We hypothesized that the relative availability of meat, indicated by contribution to the diet, would be positively related to body size and population productivity of North American brown, or grizzly, bears (*Ursus arctos*). Dietary contributions of plant matter and meat derived from both terrestrial and marine sources were quantified by stable-isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of hair samples from 13 brown bear populations. Estimates of adult female body mass, mean litter size, and population density were obtained from two field studies of ours and from other published reports. The populations ranged from largely vegetarian to largely carnivorous, and food resources ranged from mostly terrestrial to mostly marine (salmon, *Oncorhynchus* spp.). The proportion of meat in the diet was significantly correlated with mean adult female body mass (r = 0.87, P < 0.01), mean litter size (r = 0.72, P < 0.01), and mean population density (r = 0.91, P < 0.01). Salmon was the most important source of meat for the largest, most carnivorous bears and most productive populations. We conclude that availability of meat, particularly salmon, greatly influences habitat quality for brown bears at both the individual level and the population level.

Résumé : Nous avons posé en hypothèse que la disponibilité relative de chair animale, telle qu'évaluée d'après sa proportion dans l'alimentation, est probablement reliée directement à la taille corporelle et à la productivité de la population chez l'Ours brun ou Grizzli, *Ursus arctos*. Les contributions alimentaires respectives des matières végétales et animales provenant de sources terrestres et marines ont été évaluées par une analyse des isotopes stables ($\delta^{13}C$ et $\delta^{15}N$) dans des échantillons de poils prélevés chez 13 populations d'ours. Des estimations de la masse corporelle des femelles adultes, du nombre moyen de petits par portée et de la densité des populations ont été obtenues au cours de nos deux études sur le terrain et à partir de données publiées. Certaines populations étaient surtout végétariennes, d'autres surtout carnivores et leurs ressources alimentaires variaient de principalement terrestres à principalement marines (saumon, *Oncorhynchus* spp.). La proportion de tissu animal dans le régime était en corrélation significative avec la masse moyenne des femelles adultes (r = 0,87, P < 0,01), le nombre moyen de petits dans une portée (r = 0,72, P < 0,01) et la densité moyenne de la population (r = 0,91, P < 0,01). Le saumon était la principale source de chair animale pour les ours les plus gros, les plus carnivores et pour les populations les plus productives. Nous devons conclure que la disponibilité de matières animales, particulièrement la chair de saumon, améliore fortement la qualité de l'habitat des Ours bruns, autant pour les individus que pour les populations.

[Traduit par la Rédaction]

Introduction

The historic range of the North American brown, or grizzly, bear once spanned from the Arctic to central Mexico and from the Pacific Ocean to the Mississippi River (Servheen 1984). Expanding human populations and habitat loss reduced this range to much of Alaska, western Canada, and small areas in the contiguous 48 United States (Servheen 1984; U.S. Fish and Wildlife Service 1993). Because of the reduction in population size and range, the griz-

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Fig. 1. Relationship between mean body masses of adult female and adult male brown bears from 16 North American populations.

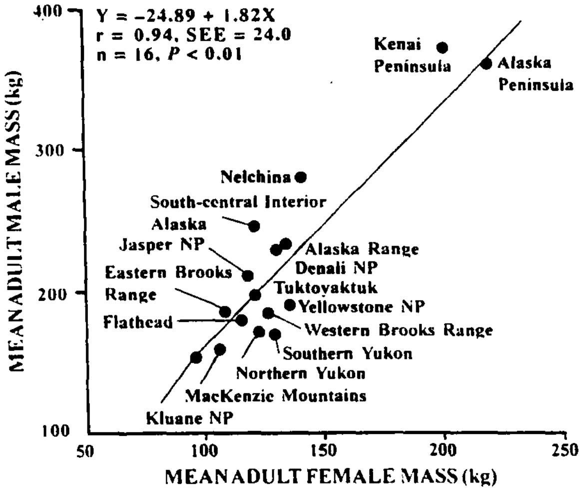
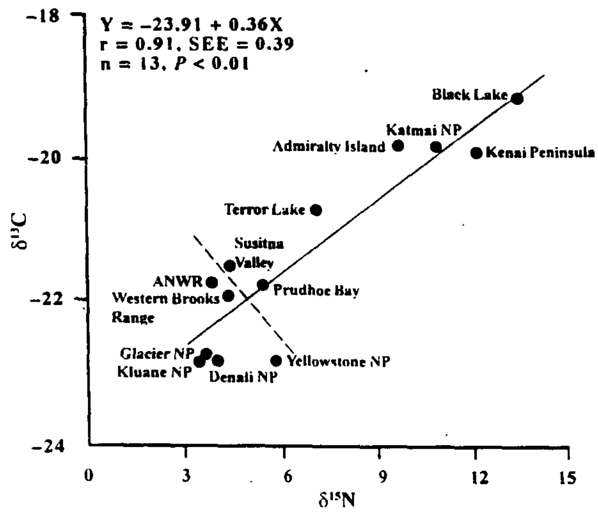


Fig. 2. Relationship between $\delta^{15}N$ and $\delta^{13}C$ signatures of hair samples from 13 North American brown bear populations. The populations above the broken line contained individuals with marine-meat dietary signatures.



The contribution of marine meat, terrestrial meat, and plant matter to brown bear diets was estimated according to Hilderbrand et al. (1996). However, as isotope signatures vary geographically (Garten 1993; Chamberlain et al. 1997), eqs. 1 and 2 of Hilderbrand et al. (1996) were modified in order to best reflect the isotope signatures of each ecosystem. Isotope signatures of the hair from large ungulates, including mule deer (*Odocoileus hemionus*), Sitka black-tailed deer (*O. hemionus sitkensis*), white-tailed deer (*O. virginianus*), elk, moose (*Alces alces*), pronghorn antelope (*Antilocapra americana*), and caribou (*Rangifer tarandus*), collected in Yellowstone National Park, Glacier National Park, the Kenai Peninsula, Admiralty Island, and the North Slope of Alaska, were used to develop herbivore base lines for each population (Barnett 1994; Ben-David et al. 1997; Jacoby 1998).

Body masses of bears captured from the Kenai Peninsula and Denali National Park populations were determined using a tripod and electronic load cell (±0.2 kg). Mean body masses, based on actual masses rather than estimates, for the other 14 populations were previously published and summarized in Blanchard (1987), Stringham (1990*b*), McLellan (1994), and McCann (1997). Adult female body masses, which were compared with litter sizes, were representative of the years during which litter size was measured and therefore may differ from the values in the above citations. When possible, the mass measurements used were those for the individuals from which hair samples were collected. If no mass measurements were available, previously published means for each population were used (Reynolds 1992; McLellan 1994; R. Sellers, personal communication). As body masses were measured at different times during the year, seasonal body mass measurements were standardized according to Stringham (1990*a*) and McLellan (1994). Mean spring litter sizes for 10 populations were obtained from Barnes and Smith (1992), Reynolds (1992), McLellan (1994), Knight et al. (1997), McCann (1997), Miller (1997), Reynolds (1997), and R. Sellers (personal communication). Density estimates for 10 populations were obtained from Knight et al. (1990), Miller and Sellers (1992), McLellan (1994), Miller et al. (1997), and Knight et al. (1997). The density of the Kenai Peninsula population was extrapolated from known densities of other populations by Del Frate (1993).

Relationships between dietary meat content, female body mass, litter size, and population density were tested using linear least squares regression analyses (Zar 1984). Density estimates for the Kenai Peninsula, Black Lake, and Yellowstone National Park populations were not included in the analyses (see the Discussion). Litter size, estimated in early spring, was chosen as the most appropriate variable for reproductive success because it should be the most sensitive to female condition in the den and therefore to the availability of food resources in the preceding year. It should also be independent of virtually all non-nutritional factors affecting bears after hibernation, such as social interactions, hunting by humans, and predation.

Results

Mean body masses of adult female and adult male brown bears were highly correlated ($P < 0.01$) and varied twofold across the species' North American range (Fig. 1; Stringham 1990*a*, 1990*b*). Adult males were, on average, 1.8 times larger than females irrespective of location. The $\delta^{13}C$ and $\delta^{15}N$ signatures of adult females were positively correlated ($P < 0.01$) because $\delta^{15}N$ increases with increasing trophic level, and both $\delta^{13}C$ and $\delta^{15}N$ increase with marine content of the diet (Hilderbrand et al. 1996). $\delta^{13}C$ and $\delta^{15}N$ values of diets ranged from very low for the interior, non-salmon-eating populations in Glacier, Kluane, and Denali National Parks to very high values for the coastal, salmon-eating Alaskan populations (Fig. 2). Yellowstone bears had the highest dietary meat contribution of all interior populations (Table 1).

Mean female body mass was positively correlated with an increasing contribution of dietary meat (Fig. 3). Coastal, salmon-eating bears were the largest and interior, vegetarian bears the smallest. Mean litter size was positively correlated with dietary meat content (Fig. 4A) and female body mass (Fig. 4B; Stringham 1990*b*; McLellan 1994). Population density was positively correlated with dietary meat contribution (Fig. 5). Most highly piscivorous coastal Alaska populations had densities as much as 55 times those of the more vegetarian interior populations. The densities of three populations (Black Lake, Kenai Peninsula, and Yellowstone National Park), however, were lower than expected. We believe that this may reflect the influence of human activities and (or) unique food conditions (see below). When coastal, salmon-eating populations (Katmai National Park, Kenai Peninsula, Black Lake, Terror Lake, and Admiralty Island) cub production that are incurred during winter dormancy (Farley and Robbins 1995). Therefore, abundant late-summer and fall salmon are more useful for the accumulation of the lipid reserves necessary for successful hibernation and cub production than are meat resources in spring, which primarily replenish lost body reserves (Hilderbrand 1998).

The three populations with a substantially lower density than would be predicted from the relative meat content of their diet (Black Lake, Kenai Peninsula, and Yellowstone National Park; Fig. 5) illustrate different constraints on brown bear populations. The Black Lake population is moderately hunted, probably reducing the density below what would be expected on the basis of available food resources (Sellers 1994). This reduction in density likely contributes to the large individual size (D. Sellers, personal communication). The Kenai Peninsula population is also hunted and is in an area of expanding residential and commercial development, increased recreational activity, and logging. Bears have been excluded from some salmon runs by intense sport fishing and development along rivers and streams, and recently, combined mortality due to hunting and kills made in defense of life and property have exceeded sustainable harvest estimates (Schwartz and Arthur 1997). Additionally, the current population estimate (Del Frate 1993) is an extrapolation from measurements from other populations and is probably conservative. As bears are restricted to increasingly fewer fishing sites, greater competition and risk of predation could prevent smaller bears and females with offspring from exploiting spawning salmon, which could lead to increased mortality (Schoen and Beier 1990; McLellan 1994; Mattson and Reinhart 1995). Thus, while some adults, particularly lone bears, continue to eat a lot of salmon, the salmon intake of the population as a whole is restricted by the number of feeding sites. Ultimately, research must be done to establish the relationships between the density of spawning salmon streams and bear access, the temporal, spatial, and biomass characteristics of spawning runs, and bear density.

The Yellowstone population is likely an example of an interior population with similar problems. The low density of this population relative to that predicted by the dietary meat contribution may be due to any or all of five possibilities: (1) the population estimates are low, (2) the population density is being depressed unnaturally by man, (3) meat resources, particularly ungulates and army cutworm moths (*Euxoa auxiliaris*) (Mattson et al. 1991*a*, 1991*b*), are more difficult to exploit efficiently than salmon, owing to spatial and temporal distribution patterns, (4) relatively little nutritious plant matter is available, so even relatively small amounts of dietary meat provide a disproportionate amount of total nutrients, and (5) the inconsistent availability of ungulate carcasses and whitebark pine seeds (*Pinus albicaulis*) across years (Mattson 1997) makes cub-rearing success highly variable. Hypotheses 3, 4, and 5 are supported by the lack of significant berry production in Yellowstone National Park relative to virtually all other ecosystems farther north where brown bears occur (Mattson et al. 1991*a*), and the small body masses of both adult male and adult female bears in Yellowstone National Park relative to those of salmon-eating bear populations (Figs. 1 and 3). We hypothesize that any reduction in available meat (i.e., ungulates, army cutworm moths, and cutthroat trout) and whitebark pine seeds would have a greater impact in Yellowstone than in other ecosystems where other nutritious alternative foods are available.

Availability of meat and (or) berries during the fall is an important management consideration in ecosystems targeted for brown bear reintroductions, such as the Bitterroot Ecosystem in central Idaho (Servheen 1984; U.S. Fish and Wildlife Service 1996). Historically, this area supported salmon (Fulton 1968, 1970) that were heavily used by brown bears when available (Hilderbrand et al. 1996). In the Bitterroot Ecosystem, the brown bear is now extinct, and the salmon nearly so. Recovery of salmon in that ecosystem could transform a reintroduced, low-density population of brown bears characterized by small individuals and low productivity to one of much higher density and with larger bears. However, salmon recovery will require a very long-term effort.

In conclusion, abundant meat resources positively affect body size, reproductive success, and population density of brown bears. Thus, purposeful management of such meat resources for bears will benefit both interior and coastal populations. As wildlife management agencies increasingly practice ecosystem management in which predators are a valued component, defining harvestable surpluses of ungulates and fish has important implications for the availability of these nutritional resources to large carnivores like brown bears, as well as to the rest of the freshwater and terrestrial ecosystem (Kline et al. 1990; Bilby et al. 1996; Ben-David et al. 1997). We conclude that the availability of dietary meat, especially salmon during late summer and fall, has a major influence on habitat quality for brown bears at both the individual level and the population level.

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