

## INTERSPECIFIC RESOURCE PARTITIONING IN SYMPATRIC URSIDS

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**Abstract.** The fundamental niche of a species is rarely if ever realized because the presence of other species restricts it to a narrower range of ecological conditions. The effects of this narrower range of conditions define how resources are partitioned. Resource partitioning has been inferred but not demonstrated previously for sympatric ursids. We estimated assimilated diet in relation to body condition (body fat and lean and total body mass) and reproduction for sympatric brown bears (*Ursus arctos*) and American black bears (*U. americanus*) in south-central Alaska, 1998–2000. Based on isotopic analysis of blood and keratin in claws, salmon (*Oncorhynchus* spp.) predominated in brown bear diets (>53% annually) whereas black bears assimilated 0–25% salmon annually. Black bears did not exploit salmon during a year with below average spawning numbers, probably because brown bears deterred black bear access to salmon. Proportion of salmon in assimilated diet was consistent across years for brown bears and represented the major portion of their diet. Body size of brown bears in the study area approached mean body size of several coastal brown bear populations, demonstrating the importance of salmon availability to body condition. Black bears occurred at a comparable density (mass:mass), but body condition varied and was related directly to the amount of salmon assimilated in their diet. Both species gained most lean body mass during spring and all body fat during summer when salmon were present. Improved body condition (i.e., increased percentage body fat) from salmon consumption reduced catabolism of lean body mass during hibernation, resulting in better body condition the following spring. Further, black bear reproduction was directly related to body condition; reproductive rates were reduced when body condition was lower. High body fat content across years for brown bears was reflected in consistently high reproductive levels. We suggest that the fundamental niche of black bears was constrained by brown bears through partitioning of food resources, which varied among years. Reduced exploitation of salmon caused black bears to rely more extensively on less reliable or nutritious food sources (e.g., moose [*Alces alces*], berries) resulting in lowered body condition and subsequent reproduction.

**Key words:** Alaska, USA; American black bear; brown bear; diet; *Oncorhynchus* spp.; resource partitioning; salmon; *Ursus americanus*; *Ursus arctos*.

### INTRODUCTION

The set of resources a species can use in the absence of competition and other biotic interactions has been defined as the fundamental niche (Krebs 2001). A species' fundamental niche is rarely achieved because the presence of other species restricts it to a narrower range of ecological conditions (Caughley and Sinclair 1994), or the realized niche. Ecologically similar species partition resources depending on several factors including species' abundance and resource availability. If the resource being partitioned is food, variation in food abundance and consequent exploitation could affect fitness and ultimately demographics of a species.

The geographic ranges of American black bears (*Ursus americanus*; see Plate 1) and brown bears (*Ursus arctos*) overlapped extensively in North America prior to European settlement (Herrero 1972). In Alaska, brown and black bears coexist throughout much of the state (Jonkel 1987, Kolenosky and Strathearn 1987), although black bears are more typically found in forest-dominated areas (Miller et al. 1997). Herrero (1978) suggested that where these two species occurred in sympatry, differences in behavior and morphology allowed brown bears to better exploit open areas whereas black bears were better adapted to more forested areas. Because of similarities between these species, Jonkel (1984) stated that niche separation must occur to allow coexistence. Many studies of sympatric brown and black bears have emphasized differences in habitat use to describe coexistence (Kasworm and Their 1990, Aune 1994, Holm et al. 1999). Other reported means of coexistence between brown and black bears include spatial separation (Aune 1994), temporal differ-

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PLATE 1. (Left) Female American black bear (*Ursus americanus*) with young, south-central Alaska. (Right) Preparing to attach GPS collar to female American black bear, south-central Alaska. Photo credit: National Park Service.

ences in activity (Shaffer 1971, Holm et al. 1999), and use of different foods (Jacoby et al. 1999).

Numerous diet studies of bears have been conducted, including studies where black and brown bears are sympatric (Lloyd and Fleck 1977, Kendall 1983, Aune 1994, Holm 1998, Jacoby et al. 1999). Considerable variation in dietary overlap can occur, ranging from extensive overlap (Aune 1994) to complete exclusion of certain food items (Jacoby et al. 1999). However, these studies did not quantify direct effects of dietary overlap on these species. Most previous studies of bear diets were based on scat analyses, which has several shortcomings including that diets are estimated at a population level rather than the individual level, highly digestible food items (e.g., meat) are underrepresented, and the nutritional importance of various food items is not incorporated (Hilderbrand et al. 1999). More recently, stable isotope analyses have been used to estimate assimilated diet of animals (Kelly 2000), including bears (Hilderbrand et al. 1996, 1999, Jacoby et al. 1999, Hobson et al. 2000). Isotopic analyses provide estimates of assimilated nutrients and can overcome some of the shortcomings of scat analyses.

Nutritional condition of female bears has been associated with several reproductive parameters including age of first reproduction, interbirth interval, litter size, sex ratio of litters, and body mass and growth of dependent young (Rogers 1976, Elowe and Dodge 1989, Hilderbrand et al. 1999). Body size has been associated with nutrition (Schroeder 1987, Cattet 1988, Hilderbrand et al. 1999) and is used similarly to make inferences about reproductive performance in bears (Stringham 1990a, b, Noyce and Garshelis 1994, Samson and Hout 1995, Hilderbrand et al. 1999). In Minnesota, Noyce and Garshelis (1994) determined that increased female black bear body size enhanced cub mass and survival (see Plate 1).

Specifically, increased intake of meat has been linked to increased body size in bears (Blanchard 1987, Stringham 1990a, Hilderbrand et al. 1999). Spawning salmon (*Oncorhynchus* spp.) are one of the most

nutrient-rich foods available to bears (Hilderbrand et al. 1999). Digestible gross energy of fish and most other meats exceeds 90% in bears, with their proteins having a true digestibility of 100% (Pritchard and Robbins 1990). In contrast, digestible gross energy of vegetation and fruits is <65% (Pritchard and Robbins 1990). Bite size and forage availability of bears with predominantly herbivorous diets can constrain ingestion rates (Welch et al. 1997), influencing growth rates and body size (Rode et al. 2001). Therefore, bears with a diet containing a high proportion of meat are typically larger and reproductively more successful than herbivorous conspecifics (Hilderbrand et al. 1999).

Hibernation also has a strong influence on body mass. Hilderbrand et al. (2000) reported brown bears losing an average of 32% of fall body mass during hibernation. Mass loss during hibernation was increased when females had dependent young. Similar results have been demonstrated for black (Rogers 1987, Farley and Robbins 1995, Barboza et al. 1997) and polar bears (*U. maritimus*; Atkinson and Ramsey 1995). Unless bears obtain high-energy food sources such as meat after den emergence, total body mass may continue to decline during spring and has been referred to as the negative foraging period (Poelker and Hartwell 1973, Noyce and Garshelis 1998). Thus, bears typically obtain the majority of their annual energy requirements during the few months each year (summer–autumn) when food is abundant, which emphasizes the importance of consuming energy-rich food.

We used isotopic analyses to estimate the assimilated diet of sympatric brown and black bears before and during spawning salmon runs and related their assimilated diet composition to body condition and reproduction. Our goal was to examine whether resource partitioning occurred between these species, and if it occurred, how it affected one or both species. Specific objectives were: (1) to estimate the seasonal assimilated diets of brown and black bears, (2) to determine if resource partitioning with brown bears precluded black bear use of a preferred food source (i.e., salmon), (3) to

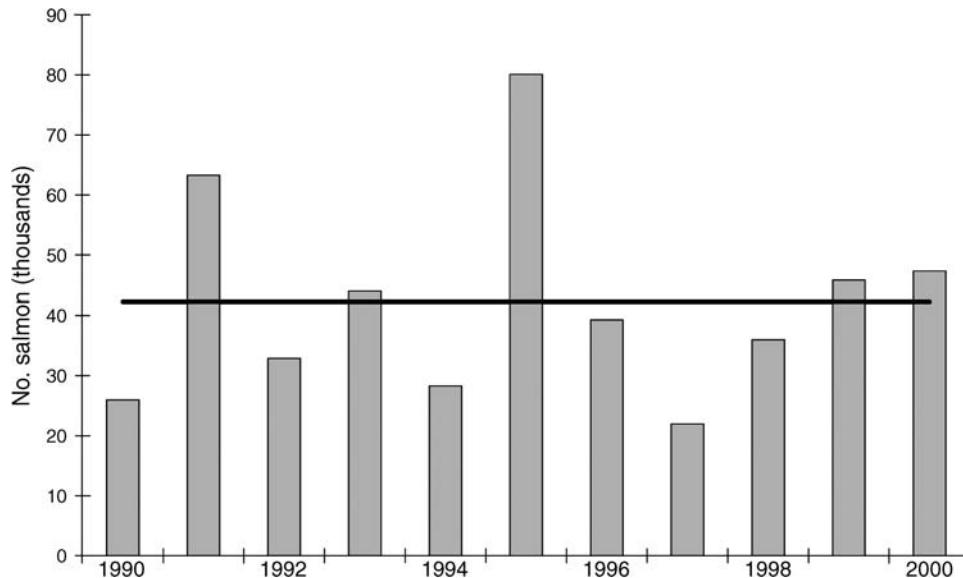


FIG. 1. Estimated number of spawning salmon entering streams within the study area, south-central Alaska, 1990–2000. The solid line represents the mean number of salmon entering the study area during 1998–1999.

assess whether body condition was influenced by proportion of salmon assimilated in the diet, (4) to quantify the effects of season and hibernation on body condition, and (5) to determine if body condition affected reproduction.

#### MATERIALS AND METHODS

The study was conducted during May–September, 1998–2000 in south-central Alaska, bounded by the Alaska Range to the north and between the Yentna and Chulitna river drainages on the west and east, respectively. The study area included the southeastern portion of Denali National Park and Preserve and Denali State Park. Elevations ranged from ~180 to 1650 m. Several medium-sized glacial-fed rivers traversed the study area. Lower elevations were characterized by spruce (*Picea glauca* and *P. mariana*), white birch (*Betula papyrifera*), and alder (*Alnus* spp.) with numerous wet meadows containing sedges and grasses. Mid-elevations (~400–800 m) contained shrub-dominated habitat including dwarf birch (*B. glandulosa*) and willow (*Salix* spp.). With the exception of stream drainages that contained shrubs or small trees, elevations >800 m were dominated by tundra, exposed rock slopes, and glaciers. Tree leaf-out at lower elevations began during mid-May; snowcover at lower elevations occurred in late September–October.

Five species of Pacific salmon (*Oncorhynchus* spp.) occurred within the study area during spawning runs (Denali National Park and Preserve, unpublished data). We summarized escapement data to estimate the number of spawning salmon that entered the study area each year (Sweet et al. 2003); the number of salmon that entered the study area was ~36 000–47 000 for 1998–2000 (Fig. 1). Moose (*Alces alces*) were the only ungulate

that occurred regularly in the study area; estimated moose density declined from 77 to 51 individuals/100 km<sup>2</sup> during 1997–2000 (Alaska Department of Fish and Game 2002). Caribou (*Rangifer tarandus*) and Dall's sheep (*Ovis dalli*) were not observed in the study area. Berry species present included blueberry (*Vaccinium* spp.) and crowberry (*Empetrum nigrum*), with soapberry (*Shepherdia canadensis*) along gravel bars of major rivers. Other vegetation important to bear diets included horsetail (*Equisetum* sp.), devil's club (*Oplopanax horridum*), ferns, grasses, and sedges.

We conducted initial flights during late April–early May each year to determine when bears vacated dens to facilitate capture. We captured bears during mid- to late May and late September 1998–2000 and during late June 1999–2000. We defined spring as May–June and summer as July–September. May captures occurred as brown bears were emerging from dens; black bears had emerged during late April. June captures occurred just before the onset of salmon spawning runs in the study area. September captures occurred prior to den entrance although many bears had moved to higher elevations where dens were ultimately located. Bears were typically in dens by mid-October.

Bears observed initially by spotters in fixed-wing aircraft were captured using immobilizing darts fired from a helicopter (Taylor et al. 1989). Adult female bears were fitted with global positioning system (GPS) or very high frequency telemetry collars (Belant and Follmann 2002; see Plate 1). All bears were monitored from the air at about two-week intervals to determine their locations (Mech 1983). GPS collars were retrieved during September captures to download location data and refurbish collars. All animal capture and handling procedures were approved by the Institutional Animal

Care and Use Committee at the University of Alaska, Fairbanks.

We recorded the presence of young observed with telemetered females by age class (cub of the year, yearling, two-year-old) during each telemetry flight and capture episode. We were confident whether or not telemetered females had dependent young; however, because of vegetation hampering observations we were not always confident of litter size.

Because of the potential importance of salmon in bear diets (Hilderbrand et al. 1999, Jacoby et al. 1999), surveys for spawning salmon were conducted using fixed-winged aircraft throughout the study area during September 2000. Salmon were assumed to occur in portions of rivers if they were observed in reaches or tributaries upstream. We reviewed unpublished data from previous salmon surveys (Alaska Department of Fish and Game, *unpublished files*; Denali National Park and Preserve, *unpublished files*) to aid in determining salmon distribution. We calculated home ranges for bears using minimum convex polygons (White and Garrott 1990) and overlaid bear home ranges on salmon distribution to determine which bears had potential access to salmon during spawning runs.

We conducted C and N isotopic analyses using red blood cells from September 1998 and keratin obtained from claws in 1999–2000 of captured bears. Red blood cells and keratin provide similar isotopic signatures (Hilderbrand et al. 1996). A 10-cm<sup>3</sup> blood sample was drawn from the femoral artery or cephalic vein and stored in a glass vial. Blood was spun at 3142 rad/s with a centrifuge, and serum was separated from clotted blood cells. Red blood cells were dried at 60–70°C and ground to a fine powder before analysis. We incrementally removed keratin samples at 3–5 mm intervals from the claw on the third digit of a front foot of individuals (K. Kielland and J. L. Belant, *unpublished data*). We used a battery-operated hand grinder with a 3 mm diameter cutting bit to remove keratin; shavings from each sample were placed in an individually labeled plastic bag. We were careful to avoid contacting the vein along the proximal portion of the claw. Growth of keratin varies seasonally (K. Kielland and J. L. Belant, *unpublished data*), similar to hair and bone (Hilderbrand et al. 1996), and appears to be based on the metabolic activity of bears. Therefore, we measured and recorded the distance from the claw to the hairline to the center of each keratin sample. Using mean seasonal claw growth rates calculated from black and brown bears in this study area (K. Kielland and J. L. Belant, *unpublished data*) and the distance from hairline to each keratin sample, we backdated from the date of capture to estimate the time at which keratin deposition occurred. Thus, we were able to use the serial samples to estimate mean seasonal assimilated diets for individual bears.

Keratin samples were ground to a fine powder and 0.1–0.4 mg per dried sample were loaded into tin boats. Isotopic analyses were conducted at the University of

Alaska Fairbanks using a Finnigan MAT ConFlo II interface (Finnigan MAT, Bremen, Germany) with a Finnigan Delta Plus mass spectrometer. We report results as ratios in parts per thousand (‰) with a reproducibility of  $\leq 0.2\%$  using the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where  $\delta X$  is  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ , and  $R$  is the  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  ratio (Peterson and Fry 1987). Results are reported relative to PeeDee Belemnite limestone ( $\delta^{13}\text{C}$ ) or atmospheric nitrogen ( $\delta^{15}\text{N}$ ).

We used blood samples or backdated keratin samples that were deposited during spring and summer to estimate the mean  $^{15}\text{N}$  and  $^{13}\text{C}$  levels as indices of assimilated diet. We used isotopic signatures of these samples to estimate the assimilated dietary contribution of salmon, terrestrial meat, and vegetation following Hilderbrand et al. (1996) and Jacoby et al. (1999). We defined dietary meat as the sum of salmon and terrestrial meat. We mathematically constrained our results such that no dietary item or sum of dietary items for an individual bear represented  $<0$  or  $>100\%$  of the assimilated diet, respectively (Jacoby et al. 1999). Analysis of covariance was used to test for relationships between years with percentage salmon in the assimilated diet during summer and percentage body fat in September.

We weighed captured bears with an electronic scale ( $\pm 0.5$  kg) and used bioelectrical impedance analysis to estimate percentage body fat of captured individuals (Farley and Robbins 1994, Hilderbrand et al. 1998a, b). Data were collected 1–5 times from individual bears; body fat estimates for individual bears were considered independent across years. We used analysis of variance (ANOVA) to compare percentage mean body fat obtained from all captures within and between species across capture months. We used repeated-measures ANOVA to compare mean body fat in individual bears captured during May, June, and September of a given year (Zar 1984). Tukey tests were used to determine which means differed. For bears captured during autumn and the following spring, relative amounts of fat and the contribution of fat to body energy losses during hibernation were estimated according to previous methods (Atkinson and Ramsay 1995, Atkinson et al. 1996). We used power regression techniques (PROC NLIN, SAS Institute 1989) to assess relationships between the relative amount of fat in autumn and the proportional contribution of fat to body mass and body energy losses. All means are reported with  $\pm \text{sd}$ ; statistical significance was set at  $\alpha = 0.05$ .

## RESULTS

We captured 46 black bears and 31 brown bears during this study; individual bears were captured 1–6 times. Samples sizes for individual tests varied as all data were not collected during each capture episode. We obtained keratin samples from 15 brown (7 and 8 in

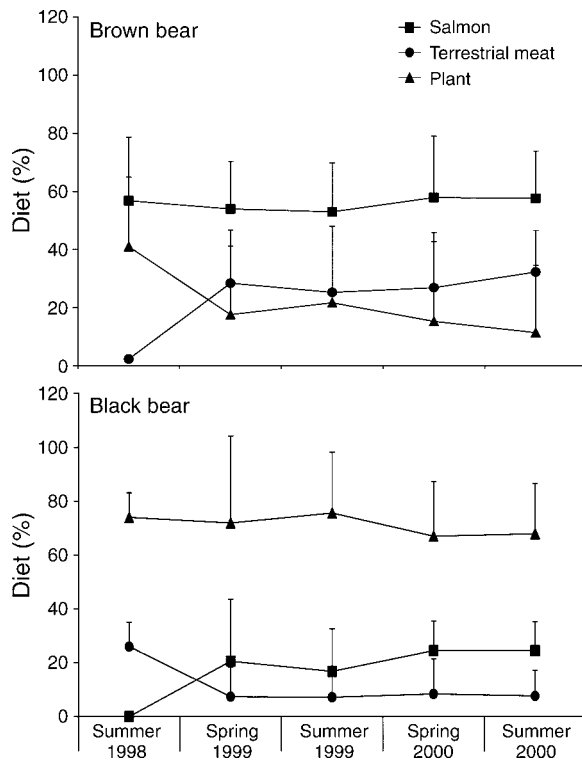


FIG. 2. Assimilated diet (mean + SD) of adult female brown bears (top panel) and American black bears (bottom panel) during spring (May–June) and summer (July–September) as estimated from isotopic signatures, south-central Alaska, 1998–2000.

1999 and 2000, respectively) and 27 black bears (16 and 11 in 1999 and 2000, respectively) and blood samples from four individuals of each species during 1998. Home ranges of all bears overlapped with rivers or streams containing salmon. Thus, all bears potentially had access to this resource during spawning runs.

Brown and black bear assimilated diets differed ( $F_{2,258} = 132.25, P < 0.001$ ). Mean assimilated dietary contribution of salmon was four times greater in brown bears than in black bears (56% vs. 14%; Fig. 2), while the assimilated dietary contributions of plants were less (25% vs. 73%;  $P < 0.05$ , Fig. 2). There was a three-way interaction of species, year, and food type ( $F_{8,252} = 3.20, P = 0.002$ ), with black bears consuming no salmon and brown bears consuming little terrestrial meat during summer 1998. Mean assimilated dietary meat was substantially higher for brown bears (84% and 75% during spring and summer, respectively) than for black bears (30% and 27%, respectively)

Neither percentage body fat during September nor salmon in the assimilated diet varied for brown bears ( $F_{3,14} = 2.26, P = 0.127$ ), but did for black bears ( $F_{3,19} = 9.92, P < 0.001$ ). For black bears, body fat was lower ( $P < 0.05$ ) in 1998 when salmon was absent from the diet.

Percentage body fat estimated from all captured individuals varied annually ( $F_{2,115} = 3.30, P = 0.040$ ) and by season ( $F_{2,115} = 125.10, P < 0.001$ , Fig. 3). In general, percentage body fat was less during 1998 than during 1999–2000. On an annual basis, percentage body fat for both species was highest during September and declined through the following June. Black bear body fat levels were lower in September 1998 than later years in contrast to brown bears, which maintained consistent body fat levels in September among years ( $F_{2,115} = 6.22,$

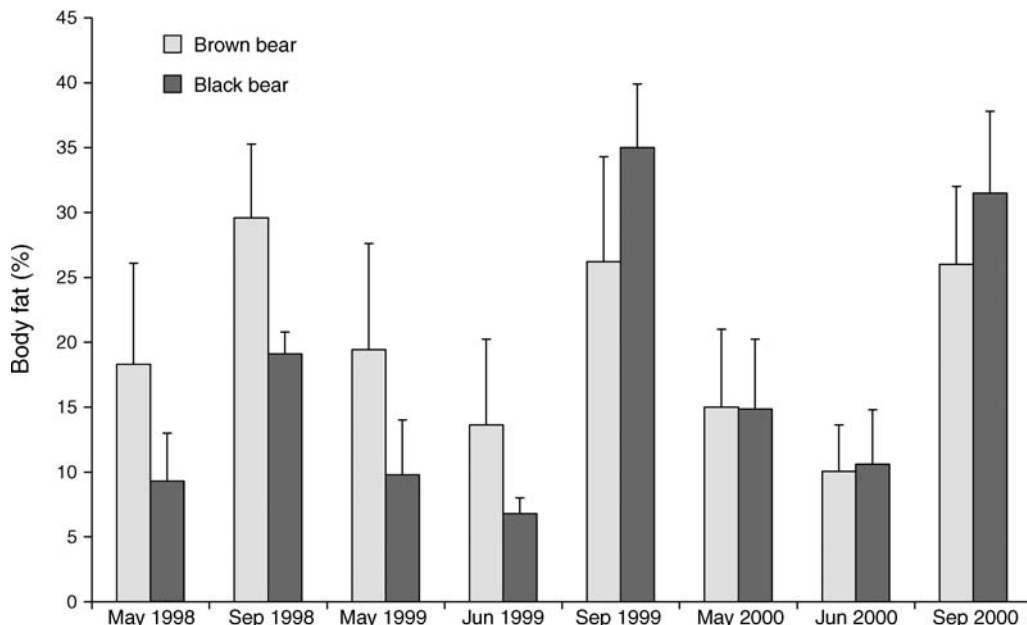


FIG. 3. Percentage body fat (mean + SD) for adult female brown and American black bears, south-central Alaska, 1998–2000.

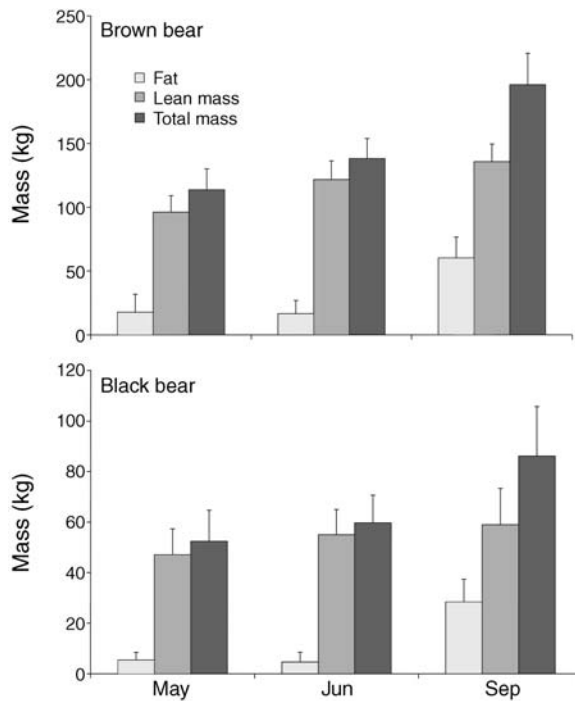


FIG. 4. Body composition (mean + SD) of adult female brown bears ( $n=6$ , top panel) and American black bears ( $n=8$ , bottom panel) by season, south-central Alaska, 1999–2000.

$P=0.003$ ). Body fat levels of black bears remained lower than that of brown bears until September 1999 ( $F_{2,115}=10.82$ ,  $P < 0.001$ ).

Seasonally, brown bears were 2.2–2.3 times larger than black bears ( $196.1 \pm 24.7$  vs.  $86.1 \pm 19.6$  kg; Fig. 4). Body mass varied seasonally (brown bears,  $F_{2,10}=141.24$ ,  $P < 0.001$ ; black bears,  $F_{2,14}=34.29$ ,  $P < 0.001$ ); for both species, body mass remained constant ( $P > 0.05$ ) during spring then increased during summer ( $P < 0.05$ ). The contribution of body fat to total body mass varied for both species (brown bears,  $F_{2,10}=34.71$ ,  $P < 0.001$ ; black bears,  $F_{2,14}=42.90$ ,  $P < 0.001$ ) during spring–summer; body fat remained constant ( $P > 0.05$ ) during spring then increased ( $P < 0.05$ ) through summer. For brown and black bears, 100% of total body mass gain attributable to fat occurred during summer. Fat represented 76% and 85% of total mass gain during summer for brown and black bears, respectively.

The contribution of lean body mass to total body mass also varied seasonally (brown bears,  $F_{2,10}=16.30$ ,  $P = 0.001$ ; black bears,  $F_{2,14}=8.26$ ,  $P = 0.004$ ). In contrast to body fat, lean body mass for both species increased ( $P < 0.05$ ) during spring then remained constant ( $P > 0.05$ ) through summer. For brown and black bears, respectively, 64% and 66% of the increases in lean body mass occurred during spring. Average body mass gain by brown and black bears was 100% lean

body mass during spring and 24% and 15% lean body mass during summer, respectively.

Ten black bears and seven brown bears were handled during autumn and the following spring (winters 1998–1999 and 1999–2000). There was no difference in percentage fat change overwinter between species ( $F_{1,13}=0.61$ ,  $P = 0.448$ ) or winters ( $F_{2,13}=3.26$ ,  $P = 0.094$ ). There was an interaction of species and winter ( $F_{2,13}=5.90$ ,  $P = 0.003$ ), with black bears losing proportionally more body fat than brown bears during winter 1998–1999 (Fig. 5).

Overall, brown bears lost  $79 \pm 31$  kg (36%  $\pm$  12%) of fall body mass overwinter; black bears lost  $25 \pm 15$  kg (30%  $\pm$  8%) of fall body mass. For brown bears, mass loss consisted of 57%  $\pm$  32% body fat and 43%  $\pm$  32% lean body mass. Black bears lost 68%  $\pm$  15% body fat and 32%  $\pm$  15% lean body mass. For both species combined, the ratio of body fat to lean body mass was  $0.39 \pm 0.18$  and was positively related to the contribution of fat to body mass loss ( $y = 89.6x^{0.20}$ ,  $r^2 = 0.30$ ,  $P < 0.001$ ; Fig. 6). The body fat/lean body mass ratio was similarly related to the contribution of fat to energy used for metabolism ( $y = 97.4x^{0.06}$ ,  $r^2 = 0.44$ ,  $P < 0.001$ ; Fig. 7). Daily mass loss was  $334 \pm 132$  g/d for brown bears and  $107 \pm 63$  g/d for black bears; length of time between captures was  $236 \pm 2$  and  $233 \pm 6$  d for brown and black bears, respectively.

The proportion of black bears not accompanied by yearling or two-year-old offspring that were observed with cubs of the year differed across years ( $\chi^2 = 10.72$ ,  $df = 2$ ,  $P = 0.005$ ), in contrast to brown bears ( $\chi^2 = 3.54$ ,  $df = 2$ ,  $P = 0.170$ ). Only 3 of 21 (14%) black bears in our sample were observed with cubs of the year in 1998–1999, compared to 10 of 15 (67%) in 2000 (Table 1). For brown bears, 3 of 6 (50%) were observed with cubs of the year during 1998–1999 vs. 3 of 9 (33%) in 2000.

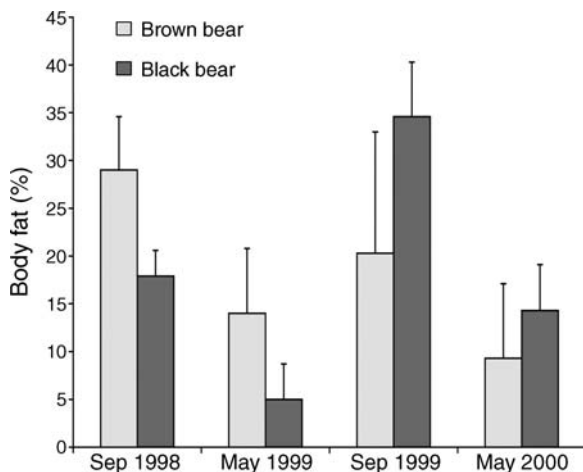


FIG. 5. Change in body composition (mean + SD) during hibernation for adult female brown bears ( $n=7$ ) and American black bears ( $n=10$ ), south-central Alaska, 1998–2000.

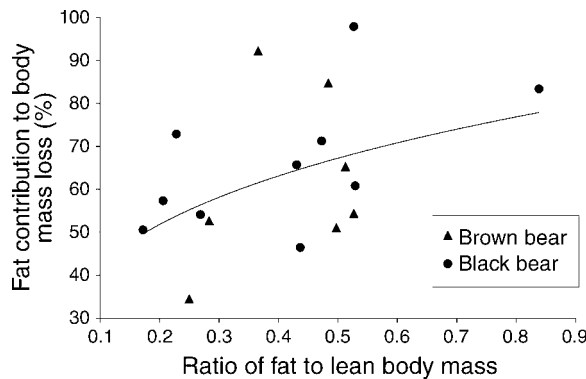


FIG. 6. Relationship between the contribution of fat to body mass loss during hibernation and the relative amount of fat in autumn (fat/lean body mass) for brown and American black bears, south-central Alaska, 1999–2000.

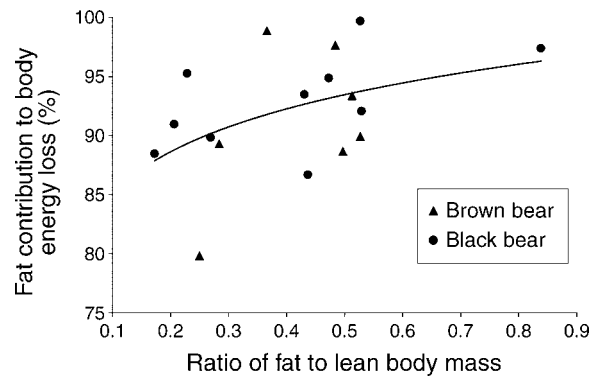


FIG. 7. Relationship between the contribution of fat to body energy loss during hibernation and the relative amount of fat in autumn (fat/lean body mass) for brown and American black bears, south-central Alaska, 1999–2000.

## DISCUSSION

### Diet

When available, salmon is probably the most important dietary item for bears (Hilderbrand et al. 1999, Jacoby et al. 1999). In our study, salmon predominated in brown bear assimilated diets but represented only 0–25% of black bear assimilated diets annually, even though all black bear had access to spawning salmon within their home ranges. Availability of salmon to black bears appeared related to the number of salmon present in the study area (Fig. 1). Low body fat content in black bears during May 1998 could have been related to very low number of salmon in the area during 1997. Based on the estimated number of salmon entering the study area each year from 1990 to 2000 (Fig. 1), we suggest that black bears had access to salmon in only about one-half of these years.

Black bears will use salmon to a greater extent than reported in this study (Jacoby et al. 1999). Where brown and black bears are sympatric, there appears to be an inverse relationship between the proportion of salmon in black bear diet and brown bear density. For example, on the Kenai Peninsula, Alaska, black bears did not use salmon when sympatric with brown bears, whereas the assimilated diet of an allopatric population of black bears on the Kenai Peninsula consisted of 53% salmon (Jacoby et al. 1999). Brown and black bear densities on portions of the Kenai Peninsula have been estimated at >200 individuals/1000 km<sup>2</sup> (Schwartz and Franzmann 1991, Del Frate 1993, as cited in Hilderbrand et al. 1999). Preliminary population estimates for brown and black bears within and adjacent to our study area were 27 and 79 individuals/1000 km<sup>2</sup>, respectively (E. Becker, unpublished data). Thus, the brown bear density and contribution of salmon to black bear assimilated diets in this study were intermediate to those described on the Kenai Peninsula (Hilderbrand et al. 1999, Jacoby et al. 1999). Brown bears are dominant to black bears and can

exclude them from preferred food sources (McLellan 1993). Despite considerably lower densities of brown bears in our study area compared to the Kenai Peninsula, interspecific resource competition probably limited black bear access to salmon.

Brown bear density was low in this study relative to the proportion of dietary salmon and total meat assimilated (see Hilderbrand et al. 1999). In contrast, mean brown bear body mass approached mean values reported for coastal areas with abundant salmon runs (Hilderbrand et al. 1999). The number of salmon entering mouths of streams along the coast is considerably greater than the number entering lower order streams further inland; our study area was >200 km from the coast. Thus, overall availability of salmon was likely limited relative to coastal areas. In our study, brown bears exploited salmon to improve individual fitness (i.e., increased body size, high percentage body fat; see Welch et al. 1997), further reducing the already low availability of salmon. The resulting limited salmon availability may account for the low brown bear density in this non-coastal area.

TABLE 1. Number of radio-collared adult female brown and American black bears observed with dependent young, south-central Alaska, May 1998–2000.

Species, year	No. females			
	Without cubs	With cubs of year	With yearlings	With two-year-olds
Brown bear				
1998	0	2	2	2
1999	3	1	3	2
2000	6	3	2	7
Black bear				
1998	3	0	4	
1999	15	3	7	
2000	5	10	1	

Use of salmon during spring by both species was unexpected. Bears and other carnivores have reportedly cached salmon or left partially consumed carcasses on land during autumn (Henry et al. 1990, Ben-David et al. 1997, Willson et al. 1998). Additional carcasses may have remained on shore adjacent to rivers; thus, bears in this study may have had access to salmon carcasses during spring. However, it is unlikely that salmon availability during spring could account for the high percentage of salmon in the spring assimilated diets. Salmon signatures in the tissues could be an artifact of sampling or isotopic analyses. Bears can lose mass after den emergence and prior to abundance of summer foods (Poelker and Hartwell 1973, Noyce and Garshelis 1998), continuing to use limited fat and lean body mass reserves. Growth of keratin in claws occurred year-round (K. Kielland and J. L. Belant, *unpublished data*) and during spring, claw growth would be based in part on nutrient reserves accumulated during the previous autumn. Thus, the isotopic values observed during spring could be based in part on salmon consumed the previous autumn. Although initiation of summer hair growth is variable, hair follicles in well-nourished bears become metabolically active during early May (Jacoby et al. 1999). Therefore, isotopic analysis of whole hair samples used in previous bear assimilated diet studies could also include diet information from the year prior to collection.

Percentage of terrestrial meat in assimilated diets of brown and black bears was within ranges found in previous studies (e.g., Holcraft and Herrero 1991, Schwartz and Franzmann 1991, Hilderbrand et al. 1996, 1999, DeBruyn 1997, Hobson et al. 2000). Assimilation of terrestrial meat by black bears was higher than brown bears during 1998 when salmon abundance was lowest. Moose were the only ungulate in our study area; the importance of moose in bear diets, particularly moose calves during spring, has been demonstrated (Larsen et al. 1989, Schwartz and Franzmann 1991, Keech et al. 2000, Bertram and Vivion 2002). Arctic ground squirrels (*Spermophilus undulatus*) occurred in portions of the study area and may have contributed to the diet of both species (Jonkel 1987, Holcraft and Herrero 1991). Ants also occurred in the study area and are important to brown and black bear diets in other parts of their range (Holcraft and Herrero 1991, DeBruyn 1997, Noyce et al. 1997, Elgmork and Unander 1998, Mattson 2001). These species may be isotopically similar to ungulates (e.g., Hobson et al. 2000) and contributed to the proportion of terrestrial meat assimilated.

#### *Body condition*

The time from den emergence to availability of abundant summer foods has been referred to as the negative foraging period (Poelker and Hartwell 1973). During this period, available food has been considered energetically inadequate to maintain body mass. Our

data do not support this hypothesis; total body mass remained constant in this study for both species during spring prior to spawning salmon runs. Previous studies have reported losses (Hellgren et al. 1989) and gains (Blanchard 1987) in bear body mass during spring. Change in body mass during spring is variable and appears related to age, sex, reproductive status, and food availability (Rogers 1976, Noyce and Garshelis 1998, Hilderbrand et al. 2000).

The majority of lean body mass was accumulated during spring. Similar results were reported in previous studies (e.g., Hilderbrand 1998, Atkinson and Ramsay 1995), which suggested that increases in lean body mass during spring provided the musculature and connective tissue necessary to support later stores of body fat. Accordingly, body fat was not accumulated until summer for either species and represented >75% of mass gains during this period. Hilderbrand (1998) reported that 80% mass gain of brown bears in fall was due to fat deposition. Availability of high quality food in fall is critical to fat deposition for use during dormancy (Farley and Robbins 1995, Barboza et al. 1997). Salmon are a nutrient-rich food (Hilderbrand et al. 1999); the high proportion of assimilated dietary salmon in brown bears we observed resulted in their consistent body fat levels during September. Although use of salmon by black bears was limited relative to brown bears, body fat was as high as brown bears from September 1999–2000. Total seasonal assimilated dietary meat for black bears was relatively constant (24–33%), suggesting suitable nutrition for growth and reproduction (Hilderbrand et al. 1999). Lower mean body fat observed in black bears during summer 1998 was associated with assimilated dietary meat of terrestrial origin. Although digestibility of terrestrial meat and salmon is similar for bears (Pritchard and Robbins 1990), terrestrial meat resources are more energetically demanding to exploit (Hilderbrand et al. 1999). Although the nutritional value of plant material is low relative to meat, because of their smaller body size, black bears can gain a significant amount of body mass with a predominantly herbivorous diet if adequate forage is available (Welch et al. 1997).

Mean daily mass loss (334 g/d) overwinter for brown bears was similar to mean mass loss (352 g/d) reported by Hilderbrand et al. (2000). Total mass loss was slightly greater in this study (36% vs. 32%) but can be attributed to the longer interval between captures in our study (236 days) vs. Hilderbrand et al. (1999; 208 days). Proportional losses of fat and lean body mass observed were also similar to brown bears in other studies (Farley and Robbins 1995, Hilderbrand et al. 2000). Direct comparisons with free-ranging black bears are unavailable; however, mean fat and lean body mass losses were similar to captive black bears (Barboza et al. 1997) and proportional to brown bears in this study.

Maintenance costs for hibernation were derived predominantly from lipid stores (Fig. 6), comparable

to other wild bear populations (Atkinson et al. 1996, Hilderbrand et al. 2000). Barboza et al. (1997) reported ~92% of energy used during hibernation for captive black bears was lipid derived. The ratio of fat to lean body mass prior to hibernation affected the proportion of fat catabolized to meet maintenance costs during hibernation in this study. Atkinson et al. (1996) and Hilderbrand et al. (2000) found similar results for polar and brown bears. In addition to increasing musculature to support body fat increases for dormancy, increased lean body mass fulfills protein demands of neonates for reproducing females (Atkinson et al. 1996). Loss of lean body mass during hibernation is related to reproductive status (Hilderbrand et al. 2000), with increased costs of protein catabolism due to lactation demands (Farley and Robbins 1995).

Overall body condition was similar for brown bears across years and probably was reflective of the high abundance of salmon in their assimilated diet. The change in body fat levels for black bears was associated with contribution of salmon in their assimilated diet, which appeared related directly to increased abundance of spawning salmon during 1999–2000. Low body fat levels in black bears during spring 1998 likely reflected low abundance of salmon in 1997 (Fig. 1). Furthermore, substantial blueberry and crowberry production was noted during September 1999–2000 captures that was not observed in 1998. With low salmon abundance, lower berry production in 1998 may have contributed to further reduce body fat levels observed in September 1998–June 1999.

#### *Effects of body condition on reproduction*

Reproductive performance of brown bears was high across years, consistent with body condition. At least one-third of captured females were observed with cubs of the year annually, similar to coastal brown bear populations (Jonkel 1987). Black bear reproduction was strongly influenced by body fat content, with twice as many females observed with cubs of the year in 2000 when percentage body fat was similar to brown bears, as in 1998–1999 when body fat levels were low. A direct relationship between body condition and reproductive performance has been demonstrated for brown and black bears in other portions of their range (e.g., Noyce and Garshelis 1994, Hilderbrand et al. 1999). Although variable, black bear interbirth intervals are typically every two years (Kolenosky and Strathearn 1987). That most black bears were observed without dependent cubs during 1998–1999 further suggests that reproductive performance may have been reduced because of comparatively poor body condition.

#### CONCLUSIONS

Salmon predominated in brown bear assimilated diets in our study area >200 km from the ocean coast, similar to coastal brown bear populations. In contrast, black bears assimilated more vegetation and appeared able to

exploit salmon only when abundance was above the long-term mean, which represented about one-half the amount of salmon exploited by an allopatric population of black bears (Jacoby et al. 1999). We suggest brown bears reduced black bear access to salmon, which caused black bears to use food sources of lower nutritional value or that required more energy to exploit. Salmon represented a majority of brown bear's assimilated diet, and overall body size of brown bears was comparable to several coastal brown bear populations, supporting the importance of salmon to body condition. Black bears were able to survive at a comparative density (based on body mass), but body condition varied in response to the amount of salmon assimilated in their diet. Both species gained a majority of lean body mass during spring and all body fat during summer when spawning salmon and berries became available. Black bear reproduction was directly related to body condition (i.e., percentage body fat), which was positively associated with salmon assimilated in their diet. Similar high body condition across years in brown bears was reflected in consistently high reproduction. Brown bears appeared to reduce the fundamental niche of black bears by altering their use of an important resource (salmon), causing black bears to rely on less available or less energy efficient food sources (e.g., moose, berries). Use of alternate foods by black bears appeared to lower their body condition and reduce reproductive output. We conclude that in this area of Alaska, brown bears formed in part the realized niche of black bears, which included partitioning and use of food resources.

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