RESOURCE PARTITIONING BY SYMPATRIC BROWN AND AMERICAN BLACK BEARS

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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. Additionally, distribution theory predicts that for two competing species living in sympatry, the subordinate species will be constrained from optimal resources. This constraint would result in use of lower quality resources by the subordinate species and possible spatial segregation from the dominant species. I evaluated diet in relation to body condition and reproduction for sympatric brown bears (*Ursus arctos*) and American black bears (*U. americanus*) in southcentral Alaska during 1998-2000, and assessed spatial segregation and habitat selection in 2000. Based on isotopic analysis, salmon (*Onchorhynchus* spp.) predominated in brown bear diets (>53% annually) whereas black bears assimilated 0-25% salmon annually. Black bears did not exploit salmon during 1998, a year with below average spawning numbers, probably because brown bears deterred black bear access to salmon. Enhanced body condition (as indexed by increased percent body fat) from salmon consumption resulted 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 poorer. Analyses of radio location data confirmed that 24-hour monitoring of bears was necessary to determine habitat use and that habitat use varied seasonally. Black bears avoided areas occupied by brown bears during summer, supporting the ideal despotic distribution model. In contrast, black bears selected areas where brown bears were present during spring, presumably because of spatially-restricted (i.e., restricted to low elevations) but dispersed availability of food. Similarities in preferred and potentially limited resources resulted in co-occupancy of areas at intermediate to coarse spatial resolutions; however, spatial avoidance of brown bears and black bears influenced population-level use of resources. Further, the realized niche of black bears was constrained by brown bears through partitioning of food resources, which varied among years. Reduced access to salmon caused black bears to forage more extensively in areas containing less nutritious food, resulting in lowered body condition and subsequent lowered reproduction. Coexistence of these species in this study area appears dependent on the distribution, abundance, and availability of salmon and berries.

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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 individual fitness and ultimately demographics of a species.

How species are distributed across a landscape can also provide insight regarding partitioning of resources between species. Spatial selection of resources is typically referred to as habitat selection (Erickson et al. 2001, Manly et al. 2002); habitat selection occurs at the individual level within a species. Fretwell (1972) originated a theory and developed two models explaining habitat selection. The ideal free distribution model states that habitat suitability is related inversely to the density of the species occupying that habitat. When animal density decreases suitability of the most suitable habitat to that of the second most suitable habitat, individuals will begin to occupy the second habitat. The ideal despotic distribution model may have application to species exhibiting territorial behavior (Fretwell 1972). In this model, aggressive behavior of individuals may force subordinate animals to occupy lower quality habitat. Applying this theory to two species implies the subordinate species would be constrained from optimal habitat by the dominant species, causing the subordinate species to use less suitable habitat.

The geographic ranges of American black (*Ursus* americanus) and brown (*U. arctos*) bears 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 forested areas (Stirling and Derocher 1990, Miller et al. 1997). Herrero (1978) suggested that 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. McLellan (1993) suggested that coexistence can occur in forested areas with diverse (e.g., ungulates, berries, salmon) and widely distributed food sources. Brown bears are considered the most dominant predator of black bears and can exclude black bears through interference competition, particularly if resources are patchy (McLellan 1993). Reported means of coexistence between brown and black bears include spatial separation (Aune 1994), temporal differences in activity (Shaffer 1971, MacHutchon et al. 1998, Holm et al. 1999), and use of different foods (Jacoby et al. 1999). Most frequently, studies of sympatric brown and black bears have emphasized differences in habitat (resource) use to describe coexistence (Kasworm and Their 1990; Aune 1994; Holm et al. 1999).

The overall goal of this project was to document how resources were partitioned by brown and American black bears in southcentral Alaska. Specifically, I investigated aspects of diet and use of habitats to address allocation of spatial and food resources. To address food resources I used isotopic analyses to estimate the assimilated diet of sympatric brown and black bears before and during spawning salmon runs. I then related the composition of their assimilated diets to body condition and reproduction. My goal was to examine whether partitioning of food resources occurred between these species, and if it occurred, how it affected one or both species. My 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 salmon, a preferred food, 3) to 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. I hypothesized that if food resources were limited, black bears would be restricted from access to salmon, reducing body condition and possibly reproductive performance.

To address spatial allocation of resources between species, I initially conducted simulations using preliminary bear telemetry data to evaluate the number of relocations necessary to estimate seasonal and pooled seasonal home ranges for individuals. I also assessed variation in diel and seasonal habitat use by individuals and species to determine necessary timing of data acquisition to ensure data collection adequately represented bear use of spatial resources. My goal was to determine sampling requirements necessary to describe black and brown bear home range and habitat use. Specific objectives were 1) to evaluate the efficacy of global positioning system (GPS) collars on black and brown bears, 2) to determine the precision of annual and seasonal home ranges using minimum convex polygon (MCP) and fixed kernel methods, and 3) to determine if habitat use differs between seasons and by time of day.

I then used categorical and continuous habitat attributes to develop population-level resource selection models for brown and American black bears. Specifically, I wanted to estimate which habitat attributes were selected seasonally by each species and whether these species were spatially segregated. Considering black bear the subordinate species (Jonkel and Cowan 1971, Murie 1981, Mattson et al. 1992), I hypothesized that black bears would avoid areas occupied by brown bears during spring and summer, following the ideal despotic distribution model (Fretwell 1972). To potentially increase support for this model, I also assessed mutual avoidance by estimating relative brown bear use of areas containing black bears.

I then tested several hypotheses related to brown and black bear seasonal use of specific habitat attributes. As brown bears in this part of Alaska den at high elevations (Miller 1990), I hypothesized seasonal nonlinear use of elevation (Waller and Mace 1997, McLellan and Hovey 2001, Nielsen et al. 2002). I expected brown bears to move from higher elevation denning areas during spring to access new growth of vegetation occurring at lower elevations (Mace and Waller 1997) and then move from lower to high elevations in late summer prior to the onset of denning. Because of the importance of salmon to brown bears (Hilderbrand et al 1999, Jacoby et al. 1999), I also hypothesized that in summer brown bears would occupy areas near streams to exploit spawning salmon.

I expected that black bears would select vegetation types in spring that contained new growth of vegetation (e.g., grasses, poplar leaves), considered important to their diet during this time of year (Kolenosky and Strathearn 1987), and that black bears would exhibit nonlinear use of elevation during summer in response to vegetation types containing berries. Specifically, I hypothesized black bears to select the dwarf shrub/herbaceous habitat that generally occurred at mid elevations. This habitat contained crowberry (*Empetrum nigrum*) and blueberry (*Vaccinium* spp.); berries are important to black bear diets throughout much of their geographic range (Kolenosky and Strathearn 1987).

References

Aune KE (1994) Comparative ecology of black and grizzly bears on the Rocky Mountain Front, Montana. Int Conf Bear Res Manage 9:365-374

Caughley G, Sinclair ARE (1994) Wildlife ecology and management. Blackwell Science, Malden, Massachusetts

Erickson WP, McDonald TL, Gerow KG, Howlin S, Kern JW (2001) Statistical issues in resource selection with radio-marked animals. In: Millspaugh JJ, Marzluff JM (eds) Radio tracking and animal populations Academic Press, San Diego, California

Fretwell SD (1972) Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey

Herrero S (1972) Aspects of evolution and adaptation in American black bears (*Ursus americanus* Pallus) and brown and grizzly bears (*Ursus arctos* Linne) of North America. Int Conf Bear Res Manage 2:221-231

Herrero S (1978) A comparison of some features of the evolution, ecology, and behavior of black and grizzly/brown bears. Carnivore 1:7-16

Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C (1999) The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Can J Zool 77:132-138

Holm GW, Lindzey FG, Moody DS (1999) Interactions of sympatric black and grizzly bears in northwest Montana. Ursus 11:99-108

Jacoby ME, Hilderbrand GV, Servheen C, Schwartz CC, Arthur SM, Hanley TA, Robbins CT, Michener R (1999) Trophic relations of brown and black bears in several North American ecosystems. J Wildl Manage 63:921-929

Jonkel CJ (1984) Grizzlies and black bear interrelationships. Spec Rep 70, Border Grizzly Proj, University of Montana, Missoula

Jonkel CJ (1987) Brown bear. In: Novak M, Baker JA, Obbard ME, Malloch B (eds) Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, pp 457-473

Jonkel CJ, Cowan IM (1971) The black bear in the spruce-fir forest. Wildl Monogr 27:1-57

Kasworm W, Their TJ (1990) Cabinet-Yaak ecosystem grizzly bear and black bear research, 1989 progress report. US Fish Wildl Serv, Missoula, Montana

Kolenosky GB, Strathearn SM (1987) Black bear. In: Novak M, Baker JA, Obbard ME, Malloch B (eds) Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, pp 443-454

Krebs CJ (2001) Ecology: the experimental analysis of distribution and abundance. Benjamin Cummings, San Francisco

Mace RD, Waller JS (1997) Final report: grizzly bear ecology in the Swan Mountains, Montana. Montana Fish, Wildlife and Parks, Helena

MacHutchon AG, Himmer S, Davis H, Gallagher M (1998) Temporal and spatial activity patterns among coastal bear populations. Ursus 10:539-546

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer, New York

Mattson DJ, Knight RR, Blanchard BM (1992) Cannibalism and predation on black bears by grizzly bears in the Yellowstone ecosystem, 1975-1990. J Mamm 73:422-425

McLellan BN (1993) Competition between black and grizzly bears as a natural population regulating factor. Western Black Bear Workshop 4:111-116

McLellan BN, Hovey FW (2001) Habitats selected by grizzly bears in a multiple use landscape. J Wildl Manage 65:92-99

Miller SD (1990) Denning ecology of brown bears in southcentral Alaska and comparisons with a sympatric black bear population. Int Conf Bear Res Manage 8:279-287

Miller SD, White GC, Sellers RA, Reynolds HV, Schoen JW, Titus K, Barnes VG, Smith RB, Nelson RR, Ballard WB, Schwartz CC (1997) Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. Wildl Monogr 133:1-55

Murie A (1981) The grizzlies of Mount McKinley. US Natl Park Serv Sci Monogr Ser 14, Washington, DC, USA

Nielsen SE, Boyce MS, Stenhouse GB, Munro RHM (2002) Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. Ursus 13:45-56

Shaffer SC (1971) Some ecological relationships of grizzly bears and black bears of the Apgar Mountains in Glacier National Park, Montana. MS thesis, University of Montana, Missoula

Stirling I, Derocher AE (1990) Factors affecting the evolution and behavioral ecology of the modern bears. Int Conf Bear Res Manage 8:189-204

Waller JS, Mace, RD (1997) Grizzly bear habitat selection in the Swan Mountains, Montana. J Wildl Manage 61:1032-1039

INTERSPECIFIC RESOURCE PARTITIONING IN SYMPATRIC URSIDS[1]

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 (*Ursus arctos*) and American black (*U. americanus*) bears in southcentral 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 (body mass:body 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

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spring and all body fat during summer when salmon were present. Improved body condition (i.e., increased percent 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 resulted in consistently high reproductive levels. We suggest the fundamental niche of black bears was constrained by brown bears whose presence reduced access to salmon for black bears, which varied among years. Reduced exploitation of salmon caused black bears to rely more extensively on less reliable (e.g., moose [*Alces alces*]) or nutritious food sources (e.g., berries) resulting in lowered body condition and subsequent reproduction.

Key Words Diet · bears · *Ursus* spp. · salmon · *Oncorhynchus* spp.

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 individual fitness and ultimately demographics of a species.

The geographic ranges of American black and brown bears overlapped extensively in North America prior to European settlement (Herrero 1972). 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. In Alaska, brown and black bears still coexist throughout much of the state (Kolenosky and Strathearn 1987; Jonkel 1987), although black bears are more typically found in forest-dominated areas (Miller et al. 1997). Many studies of sympatric brown and black bears have emphasized differences in habitat use to explain 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 differences 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 areas where black and brown bears are sympatric (Lloyd and Fleck 1977; Kendall 1983; Holm 1998; Aune 1994; 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 individuals of either species. Most previous studies of bear diets were based on scat analyses, which has several shortcomings including 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 individuals 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.

Several reproductive parameters including age of first reproduction, interbirth interval, litter size, sex ratio of litters, and body mass and growth of dependent young have been associated with nutritional condition of female bears (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.

Specifically, increased intake of meat has been linked to increased body size in bears (Blanchard 1987; Stringham 1990a; Hilderbrand et al. 1999). Spawning salmon (*Oncoryhnchus* 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 fish and other meat 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 by, and forage availability to, 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 lose an average of 32% of fall body mass during hibernation. Weight loss of adult females during hibernation was increased when they 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. This decline in body mass has been referred to as the negative foraging period (Poelker and Hartwell 1973; Noyce and Garshelis 1998). Consequently, 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 during that period.

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 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 southcentral Alaska, bounded by the Alaska Range to the north and between the Yentna and Chulitna rivers 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 about 180-1,650 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 (A*lnus* spp.) with numerous wet meadows containing sedges and grasses. Mid elevations (about 400-800 m) contained shrub-dominated habitat including dwarf birch (*B. nana*) and willow (*Salix* spp.). With the exception of stream drainages which 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 first 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, unpubl. 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 about 36,000-47,000 for 1998-2000 (Fig. 1.1). 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^2 during 1997-2000 (Alaska Department of Fish and Game 2002). Caribou (*Rangifer tarandus*) and Dall's sheep (*Ovis dalli*) were not observed but may occasionally occur in the study area. Berry species present included blueberry (*Vaccinium* spp.) and crowberry (*Empetrum nigrum*), with soapberry (*Sheperdia 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. In 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 already 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). All bears were monitored from the air at about 2-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, 2-year-old) during each telemetry flight and capture episode. We were confident whether telemetered females had dependent young; however, because vegetation sometimes hampered 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, unpubl. files; Denali National Park and Preserve, unpubl. 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-cc blood sample was drawn from the femoral artery or cephalic vein and stored in a glass vial. Blood was spun at 3,142 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 (Kielland and 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 (Kielland and 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 at 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 (Kielland and 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 ≤ 0.2‰ using the equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1{,}000,$$

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

We used blood samples or backdated keratin samples that were deposited during spring and summer to estimate the mean ^{15}N and ^{13}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 also defined total dietary meat as the sum of salmon and terrestrial meat. We mathematically constrained the 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 differences between years in 1) percent salmon in the assimilated diet during summer and 2) percent body fat in September.

We weighed captured bears with an electronic scale (±0.5 kg) and used bioelectrical impedance analysis to estimate percent 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 percent 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 using previously published methods (Atkinson and Ramsay 1995; Atkinson et al. 1996). We used power regression techniques (PROC NLIN, SAS Institute, Inc. 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 ± 1 standard deviation (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 information was not collected during each capture episode. We obtained keratin samples from 15 brown bears (7 and 8 in 1999 and 2000, respectively) and 27 black bears (16 and 11 in 1999 and 2000, respectively) and blood samples from 4 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.

Assimilated diets of brown and black bears differed (F = 132.25; 2, 258 df; $P < 0.001$). Mean assimilated dietary contribution of salmon was 4 times greater in brown bears than in black bears (56% vs. 14%; Fig. 1.2), while the assimilated dietary contributions of plants was less (25% vs. 73%; $P < 0.05$; Fig. 1.2). There was a three way interaction of species, year, and foodtype (F = 3.20; 8,252 df; $P = 0.002$), 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 percent body fat during September nor salmon in the assimilated diet varied across years for brown bears (F = 2.26; 3,14 df; $P = 0.127$), but did for black bears (F = 9.92; 3,19 df; $P < 0.001$). For black bears, body fat was lower ($P < 0.05$) in 1998 when salmon was absent from the diet.

Percent body fat estimated from all captured individuals varied annually (F = 3.30; 2, 115 df; $P = 0.040$) and by season ($F = 125.10$; 2, 115 df; $P < 0.001$) (Fig. 1.3). In general, percent body fat was less during 1998 than during 1999-2000. On an annual basis, percent body fat for both species was highest in September and declined through the following June. Black bear body fat levels in September were lower in 1998 than later years in contrast to brown bears which maintained consistent body fat levels in September among years ($F = 6.22$; 2, 115 df; $P = 0.003$). Body fat levels of black bears remained lower than that of brown bears from September 1998 until September 1999 (F = 10.82; 2, 115 df; $P < 0.001$).

Overall, brown bears were 2.2-2.3 times heavier than black bears (196.1 ± 24.7 vs. 86.1 ± 19.6 kg; Fig. 1.4). Body mass varied seasonally (brown bears: F = 141.24; 2,10 df; $P < 0.001$, black bears: F = 34.29; 2, 14 df; $P < 0.001$); 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 within each species (brown bears: F = 34.71; 2,10 df; $P < 0.001$, black bears: F = 42.90; 2, 14 df; $P < 0.001$) 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 weight 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 = 16.30; 2, 10 df; $P = 0.001$, black bears: F = 8.26; 2, 14 df; $P = 0.004$). 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. Sixty-four and 66% of the increases in lean body mass occurred during spring for brown and black bears, respectively. 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 7 brown bears were handled during autumn and the following spring (winters 1998-1999 and 1999-2000). There was no difference in percent fat change over winter between species (F = 0.61; 1, 13 df; $P = 0.448$) or winters (F = 3.26; 1, 13 df; $P = 0.094$). There was an interaction of species and winter (F = 5.90; 1, 13 df; $P = 0.003$), with black bears losing proportionally more body fat than brown bears during winter 1998-1999 (Fig. 1.5).

Overall, brown bears lost 79 ± 31 kg (36 ± 12%) of fall body mass overwinter; black bears lost 25 ± 15 kg (30 ± 8%) of fall body mass. For brown bears, mass loss consisted of 57 ± 32% body fat and 43 ± 32% lean body mass. Black bears lost 68 ± 15% body fat and 32 ± 15% lean body mass. For both species combined, the ratio of body fat to lean body mass was 0.39 ± 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. 1.6). 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. 1.7). Daily mass loss was 334 ± 132g/day for brown bears and 107 ± 63g/day for black bears; length of time between captures was 236 ± 2 and 233 ± 6 days for brown and black bears, respectively.

The proportion of black bears not accompanied by yearling or 2 year old offspring that was observed with cubs of the year differed across years ($\chi^2 = 10.72$, 2 df, $P = 0.005$), in contrast to brown bears ($\chi^2 = 3.54$, 2 df, $P = 0.170$). Only 3 of 21 (14%) black bears in the sample were observed with cubs of the year in 1998-1999, compared to 10 of 15 (67%) in 2000 (Table 1.1). For brown bears, 3 of 6 (50%) were observed with cubs of the year during 1998-1999 vs. 3 of 9 (33%) in 2000.

Discussion

Diet

When available, salmon is probably the most important dietary item for bears (Hilderbrand et al. 1999; Jacoby et al. 1999). In this study, salmon predominated in brown bear assimilated diets but represented only 0-25% of black bear assimilated diets annually, even though all black bear potentially 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. 1.1). 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 1990-2000 (Fig. 1.1), we suggest that black bears had access to salmon in only about 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/1,000 km^2 (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/1,000 km^2, respectively (E. Becker, Alaska Department of Fish and Game, 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 (Jacoby et al. 1999; Hilderbrand 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 this study area than on 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 farther inland; our study area was >200 km from the coast. Thus, overall availability of salmon was likely limited relative to coastal areas. In this study, brown bears exploited salmon to improve individual fitness (i.e., increased body size, high percent 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.

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 proportion of salmon in the spring assimilated diets. Salmon signatures in the tissues could be an artifact of sampling or isotopic analyses. Bears can lose weight 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 (Kielland and 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 timing of 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 signatures from the year prior to collection.

Percent 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 was higher by black bears than brown bears during 1998 when salmon abundance was lowest. Moose were the only ungulate in the 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 between den emergence and the 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 does 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 gain was accumulated during spring. Similar results were reported in previous studies (e.g., Hilderbrand 1988; 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 weight 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 hibernation (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 resulted in brown bear's having consistently high body fat levels during September. Although use of salmon by black bears was limited relative to that by 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 higher levels of 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 weight loss (334g/day) over winter for brown bears was similar to mean weight loss (352g/day) reported by Hilderbrand et al. (2000). Total weight loss was slightly greater in this study (36 vs. 32%) but can be attributed to the longer interval between captures in this study (236 days) vs. Hilderbrand et al. (1999; 208 days). Proportional losses of fat and lean body mass observed were also similar to those of 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 losses in captive black bears (Barboza et al. 1997) and proportional to losses in brown bears in this study.

Maintenance costs for hibernation were derived predominantly from lipid stores (Fig. 1.6), comparable to other wild bear populations (Atkinson et al. 1996; Hilderbrand et al. 2000). Barboza et al. (1997) reported about 92% of energy used during hibernation by 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 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 consistently high abundance of salmon in their assimilated diet. The annual differences in body fat levels for black bears were 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. 1.1). 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 through June 1999.

Effects of Body Condition on Reproduction

Reproductive success 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 percent body fat was similar to that in brown bears, as in 1998-1999 when body fat levels were low. A positive 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 2 years (Kolenosky and Strathearn 1987). That most black bears were observed without dependent cubs in either 1998 or 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 salmon in 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 half the amount of salmon exploited by an allopatric population of black bears (Jacoby et al. 1999). We suggest brown bear presence 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 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., percent 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 reduced in part the realized niche of black bears, which included partitioning and use of food resources.

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References

Alaska Department of Fish and Game (2002) Moose management report of survey-inventory activities 1 July 1999-30 June 2001. Project 1.0, Juneau, Alaska, USA

Atkinson SN, Nelson RA, Ramsay MA (1996) Changes in the body composition of fasting polar bears (*Ursus maritimus*): the effect of relative fatness on protein conservation. Physiol Zool 69:304-316

Atkinson SN, Ramsay MA (1995) The effect of prolonged fasting on the body composition and reproductive success of female polar bears (*Ursus maritimus*). Funct Ecol 9:559-567

Aune KE (1994) Comparative ecology of black and grizzly bears on the Rocky Mountain Front, Montana. Int Conf Bear Res Manage 9:365-374

Barboza PS, Farley SD, Robbins CT (1997) Whole-body urea cycling and protein turnover during hyperphagia and dormancy in growing bears (*Ursus americanus* and *U. arctos*). Can J Zool 75:2129-2136

Belant JL, Follmann EH (2002) Sampling considerations for American black and brown bear home range and habitat use. Ursus 13:153-169

Ben-David M, Hanley TA, Klein DR, Schell DM (1997) Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon. Can J Zool 75:803-811

Bertram MR, Vivion MT (2002) Moose mortality in eastern interior Alaska. J Wildl Manage 66:747-756

Blanchard BM (1987) Size and growth patterns of the Yellowstone grizzly bear. Int Conf Bear Res Manage **7**:99-107

Cattet M. (1988) Predicting nutritional condition in black bears and polar bears on the basis of morphological and physiological measurements. Can J Zool 68:32-39

Caughley G, Sinclair ARE (1994) Wildlife ecology and management. Blackwell Science, Malden, Massachusetts

DeBruyn TD (1997) Habitat use, food habits and population characteristics of female black bears in the central Upper Peninsula of Michigan: a geographic information system approach. PhD thesis, Michigan Technological University, Houghton

Elgmork K, Unander S (1998) Brown bear use of ant mounds in Scandinavia. Ursus 10:269-274

Elowe KD, Dodge WE (1989) Factors affecting black bear reproductive success and cub survival. J Wildl Manage 53:962-968

Farley SD, Robbins CT (1994) Development of two methods to estimate body composition of bears. Can J Zool 72:220-226

Farley SD, Robbins CT (1995) Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can J Zool 73:2216-2222

Hellgren EC, Vaughan MR, Kirkpatrick RL (1989) Seasonal patterns in physiology and nutrition of black bears in Great Dismal Swamp, Virginia-North Carolina. Can J Zool 67:1837-1850.

Henry SE, Raphael MG, Ruggiero LF (1990) Food caching and handling by marten. Great Basin Nat 50:381-383

Herrero S (1972) Aspects of evolution and adaptation in American black bears (*Ursus americanus* Pallus) and brown and grizzly bears (*Ursus arctos* Linne') of North America. Int Conf Bear Res Manage 2:221-231

Herrero S (1978) A comparison of some features of the evolution, ecology, and behavior of black and grizzly/brown bears. Carnivore 1:7-16

Hilderbrand GV (1998) Studies of the nutritional ecology of brown bears. PhD thesis, Washington State University, Pullman

Hilderbrand GV, Farley SD, Robbins CT, Hanley TA, Titus K, Servheen C (1996) Use of stable isotopes to determine diets of living and extinct bears. Can J Zool 74:2080-2088

Hilderbrand GV, Farley SD, Robbins CT (1998*a*) Predicting body condition of bears via two field methods. J Wildl Manage 62:406-409

Hilderbrand GV, Robbins CT, Farley SD (1998*b*) Determination of body composition of black and brown bears. Bear Res Education Conserv Center, Washington State University, Pullman

Hilderbrand GV, Schwartz CC, Robbins CT, Hanley TA (2000) Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. J Wildl Manage 64:178-183

Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C (1999) The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Can J Zool 77:132-138.

Hobson KA, McLellan BN, Woods JG (2000) Using stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River basin, British Columbia. Can J Zool 78:1332-1339

Holcraft AC, Herrero S (1991) Black bear, *Ursus americanus*, food habits in southwestern Alberta. Can Field-Nat 105:335-345

Holm GW (1998) Interactions of sympatric black and grizzly bears in northwest Wyoming. MS thesis, University of Wyoming, Laramie

Holm GW, Lindzey FG, Moody DS (1999) Interactions of sympatric black and grizzly bears in northwest Montana. Ursus 11:99-108

Jacoby ME, Hilderbrand GV, Servheen C, Schwartz CC, Arthur SM, Hanley TA, Robbins CT, Michener R (1999) Trophic relations of brown and black bears in several North American ecosystems. J Wildl Manage 63:921-929

Jonkel CJ (1984) Grizzlies and black bear interrelationships. Spec Rep 70, Border Grizzly Proj, University of Montana, Missoula

Jonkel CJ (1987) Brown bear. In: Novak M, Baker JA, Obbard ME, Malloch B (eds) Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, pp 457-473

Kasworm W, Their TJ (1990) Cabinet-Yaak ecosystem grizzly bear and black bear research, 1989 progress report. US Fish Wildl Serv, Missoula, Montana

Keech MA, Bowyer RT, Ver Hoef JM, Boertje RD, Dale BW, Stephenson TR (2000) Life-history consequences of maternal condition in Alaskan moose. J Wildl Manage 64:450-462

Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can J Zool 78:1-27

Kendall KC (1983) Use of pine nuts by grizzly and black bears in the Yellowstone area. Int Conf Bear Res Manage 5:166-173

Kolenosky GB, Strathearn SM (1987) Black bear. In: Novak M, Baker JA, Obbard ME, Malloch B (eds) Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, pp 443-454

Krebs CJ (2001) Ecology: the experimental analysis of distribution and abundance. Benjamin Cummings, San Francisco

Larsen DG, Gauthier DA, Markel RL (1989) Causes and rate of moose mortality in the southwest Yukon. J Wildl Manage 53:548-557

Lloyd K, Fleck S (1977) Some aspects of the ecology of black and grizzly bears in southeastern British Columbia. British Columbia Fish Wildl Branch, Victoria

Mattson DJ (2001) Myrmecophagy by Yellowstone grizzly bears. Can J Zool 79:779-793

McLellan BN (1993) Competition between black and grizzly bears as a natural population regulating factor. Western Black Bear Workshop 4:111-116

Mech LD (1983) A handbook of animal radio-tracking. University Minnesota Press, Minneapolis

Miller SD, White GC, Sellers RA, Reynolds HV, Schoen JW, Titus K, Barnes VG, Smith RB, Nelson RR, Ballard WB, Schwartz CC (1997) Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. Wildl Monogr 133:1-55

Noyce KV, Garshelis DL (1994) Body size and blood characteristics as indicators of condition and reproductive performance in black bears. Int Conf Bear Res Manage 9:481-496

Noyce KV, Garshelis DL (1998) Spring weight changes in black bears in north central Minnesota: the negative foraging period revisited. Ursus 10:521-531

Noyce KV, Kannowski PB, Riggs MR (1997) Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. Can J Zool 75:1671-1686

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Ann Rev Ecol System 18:293-320

Poelker RJ, Hartwell HD (1973) Black bear of Washington. Washington State Game Dep Biol Bull 14, Olympia

Pritchard GT, Robbins CT (1990) Digestive and metabolic efficiencies of grizzly and black bears. Can J Zool 68:1645-1651

Rode KD, Robbins CT, Shipley LA (2001) Constraints on herbivory by grizzly bears. Oecologia 128:62-71

Rogers LL (1976) Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Trans N Am Wildl Nat Resour Conf 41:431-438

Rogers LL (1987) Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildl Monogr 97:1-72

Samson C, Hout J (1995) Reproductive biology of female black bears in relation to body size in early winter. J Mammal 76:68-77

SAS Institute Inc (1989) SAS/STAT user's guide. Ver 6, Fourth Ed. SAS Institute Inc, Cary, North Carolina

Schroeder MT (1987) Blood chemistry, hematology, and condition evaluation of black bears in north coastal California. Int Conf Bear Res Manage 7:333-349

Schwartz CC, Franzmann AW (1991) Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildl Monogr 113:1-58

Shaffer SC (1971) Some ecological relationships of grizzly bears and black bears of the Apgar Mountains in Glacier National Park, Montana. MS thesis, University of Montana, Missoula

Stringham SF (1990*a*) Grizzly bear reproductive rate relative to body size. Int Conf Bear Res Manage 8:433-443

Stringham SF (1990*b*) Black bear reproductive weight relative to body weight in hunted populations. Int Conf Bear Res Manage 8:425-442

Sweet D, Ivey S, Rutz D (2003) Area management report for the recreational fisheries of northern Cook Inlet, 2002. Fish Manage Rep, Alaska Department of Fish and Game, Anchorage

Taylor WP, Reynolds III HV, Ballard WB (1989) Immobilization of grizzly bears with tiletamine hydrochloride and zolazepam hydrochloride. J Wildl Manage 53:978-981

Welch CA, Keay J, Kendall KC, Robbins CT (1997) Constraints on frugivory by bears. Ecology 78:1105-1119

White GC, Garrott RA (1990) Analysis of wildlife radio-tracking data. Academic Press, San Diego, California

Willson MF, Gende SM, Marston BH (1998) Fishes and forests. Bioscience 48:455-462

Zar JH (1984) Biostatistical analysis. Second ed. Prentice Hall, Englewood Cliffs, New Jersey

Table 1.1 Number of radiocollared adult female brown and American black bears observed with dependent young, southcentral Alaska, May 1998-2000.

		Number of females:			
Species	Year	Without cubs	With cubs of year	With yearlings	With 2-year-olds
Brown	1998	0	2	2	2
	1999	3	1	3	2
	2000	6	3	2	7
Black	1998	3	0	4	
	1999	15	3	7	
	2000	5	10	1	

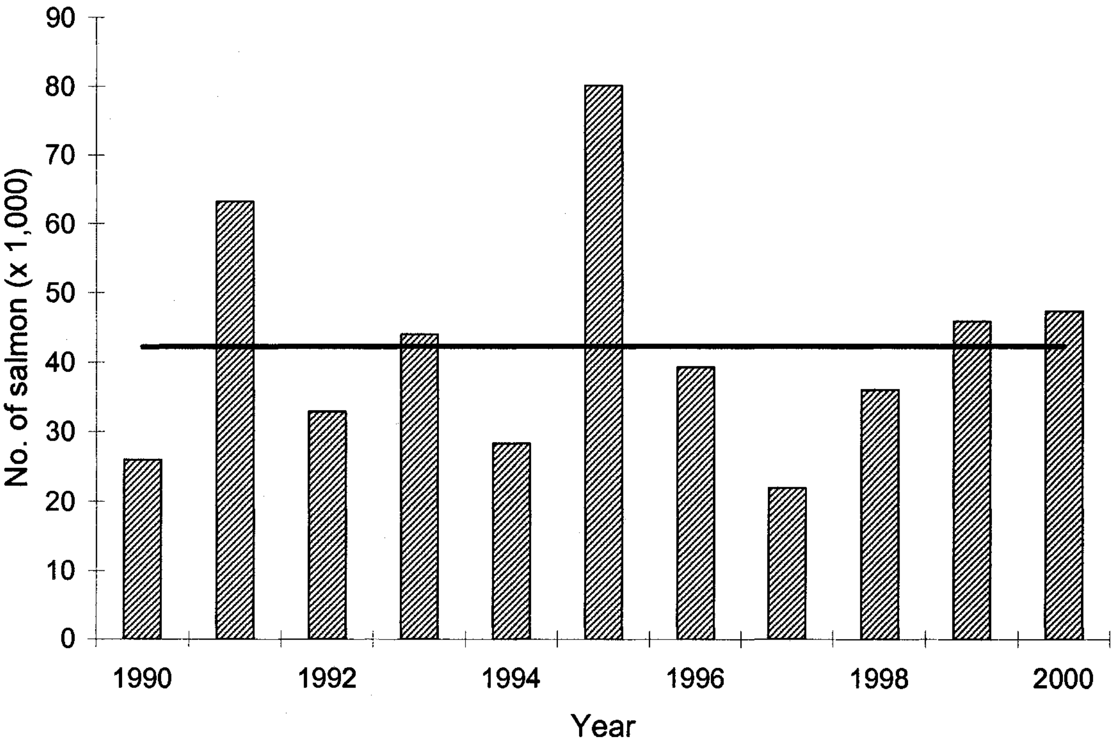

Fig. 1.1 Estimated number of spawning salmon entering streams within the study area, southcentral Alaska, 1990-2000. Solid line represents the mean number of salmon entering the study area during 1998-2000.

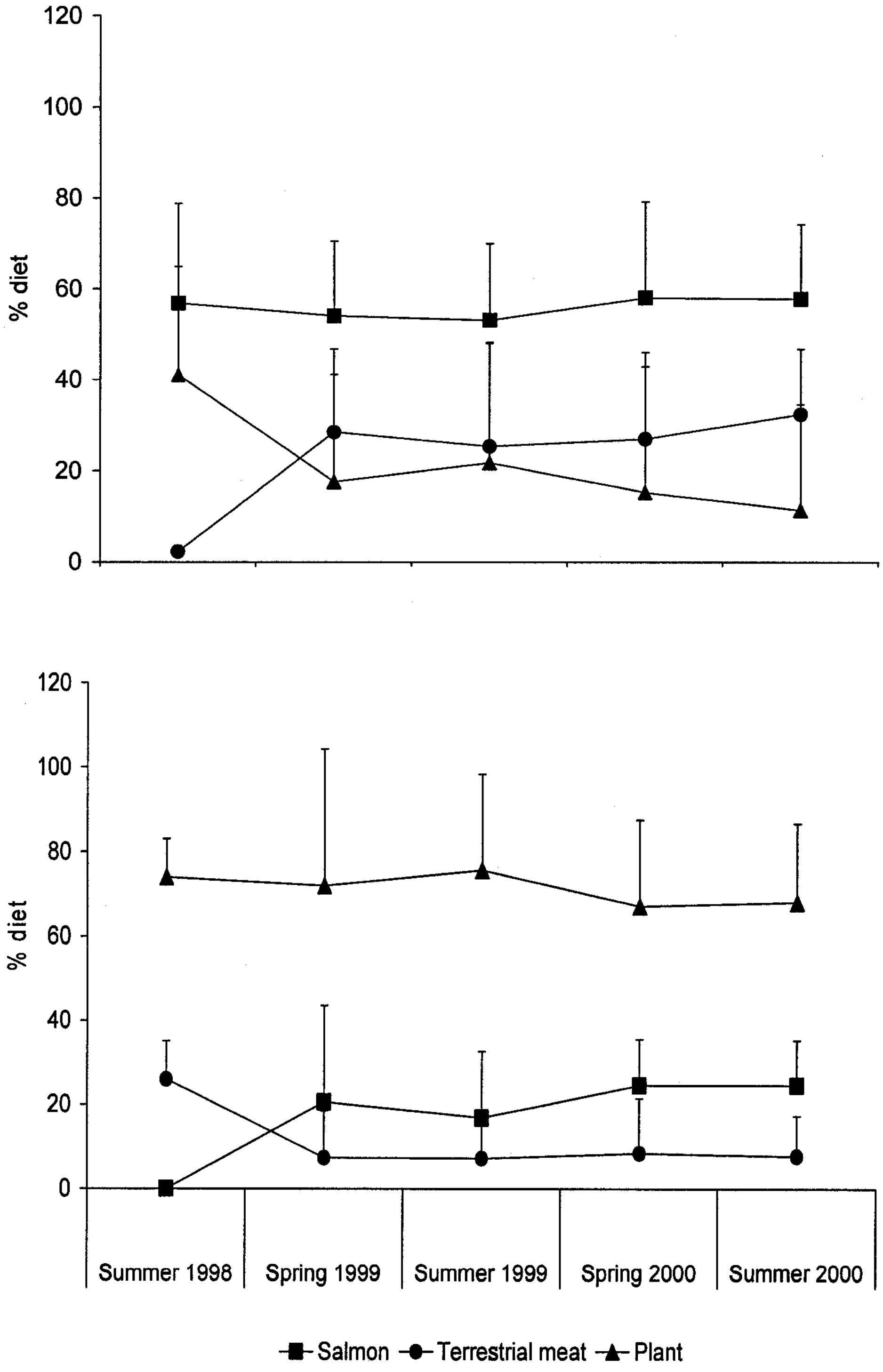

Fig. 1.2 Mean (± SD) assimilated diet of adult female brown (top panel) and American black bears (bottom panel) during spring (May-June) and summer (July-September) as estimated from isotopic signatures, southcentral Alaska, 1998-2000.

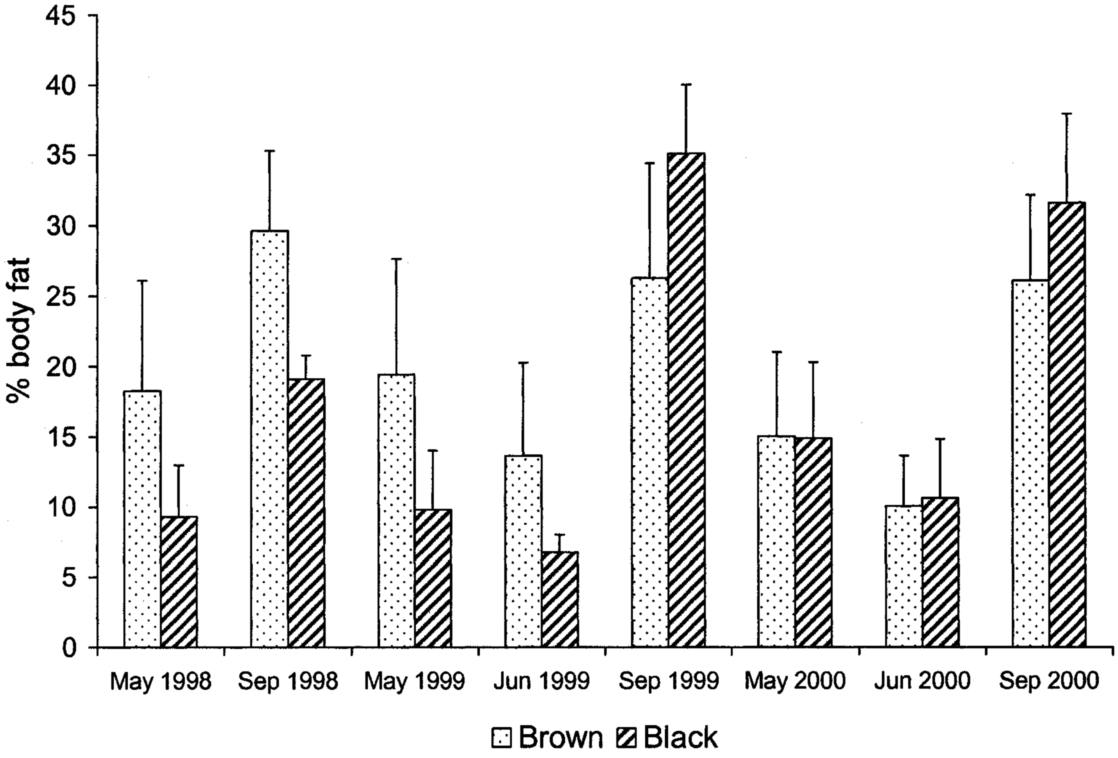

Fig. 1.3 Mean (± SD) percent body fat for adult female brown and American black bears, southcentral Alaska, 1998-2000.

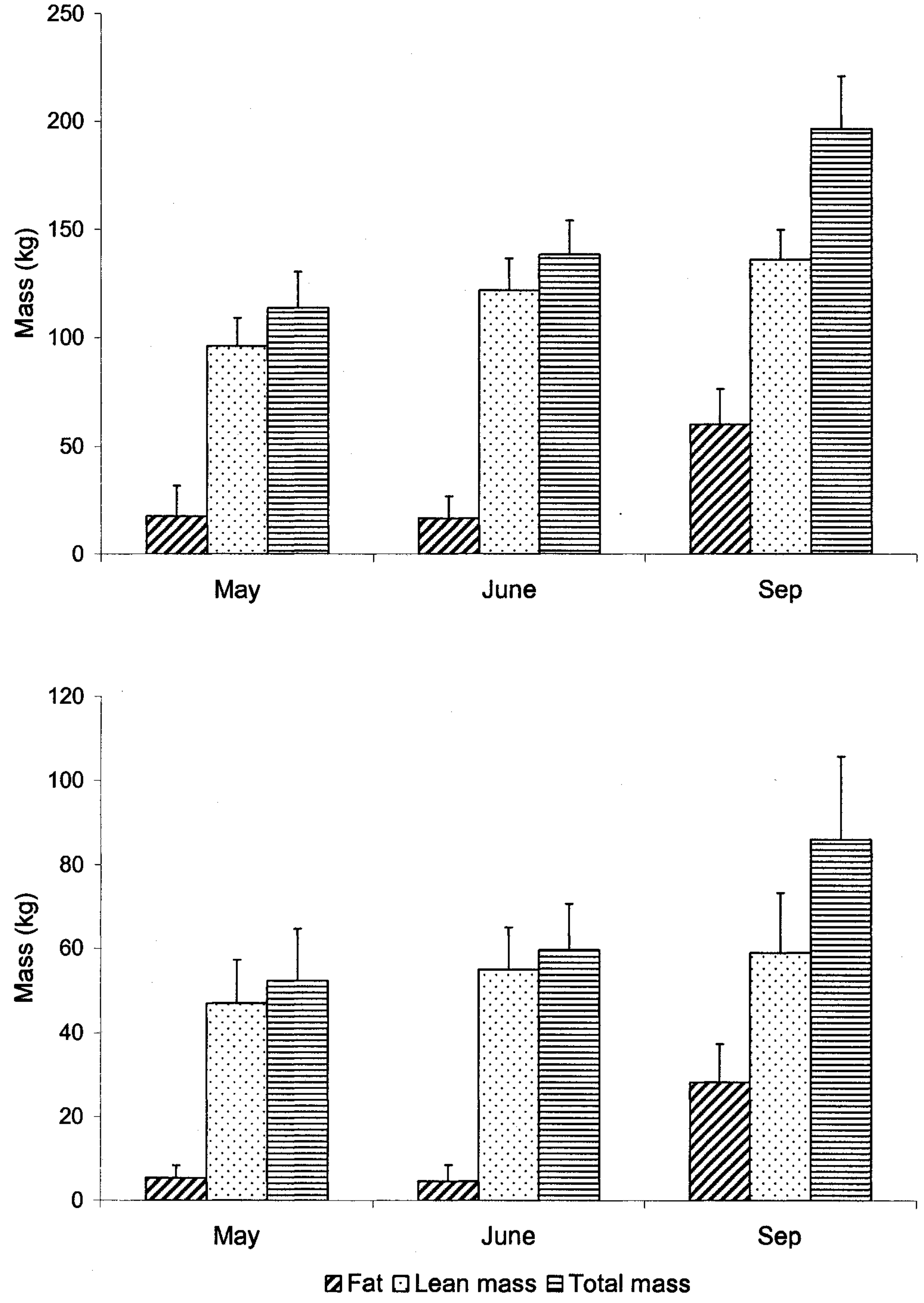

Fig. 1.4 Mean (± SD) body composition of adult female brown ($n = 6$, top panel) and American black ($n = 8$, bottom panel) bears by season, southcentral Alaska, 1999-2000.

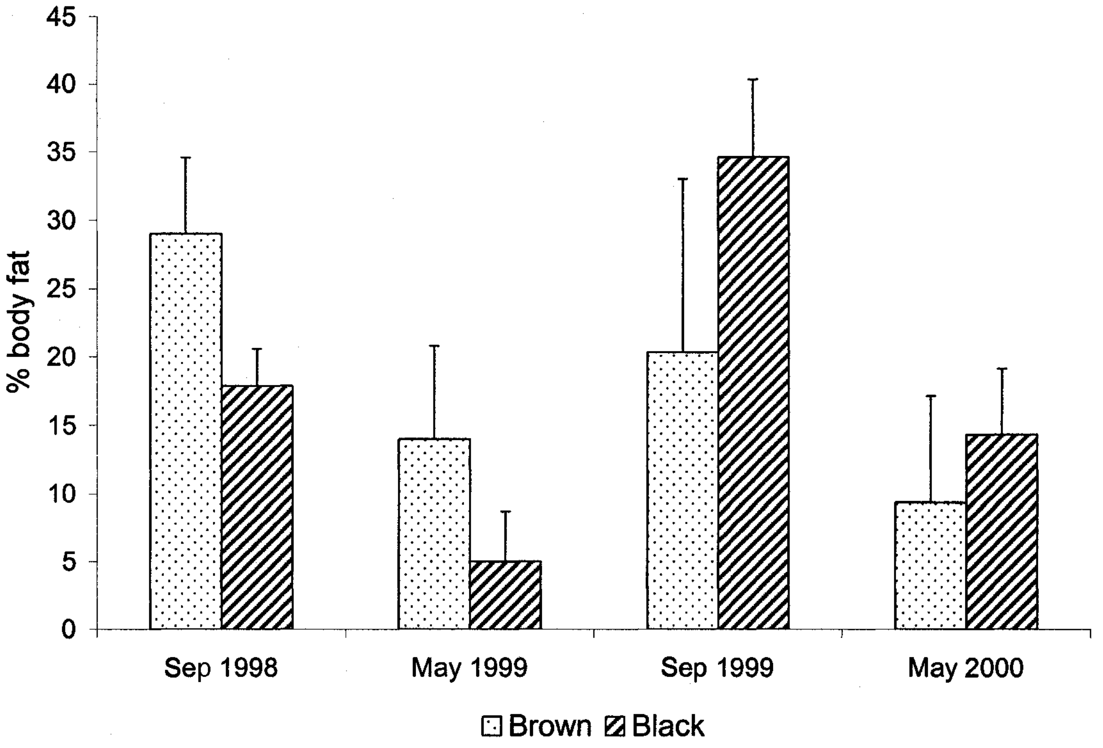

Fig. 1.5 Change in mean (± SD) body composition during hibernation for adult female brown (*n* = 7) and American black (*n* = 10) bears, southcentral Alaska, 1998-2000.

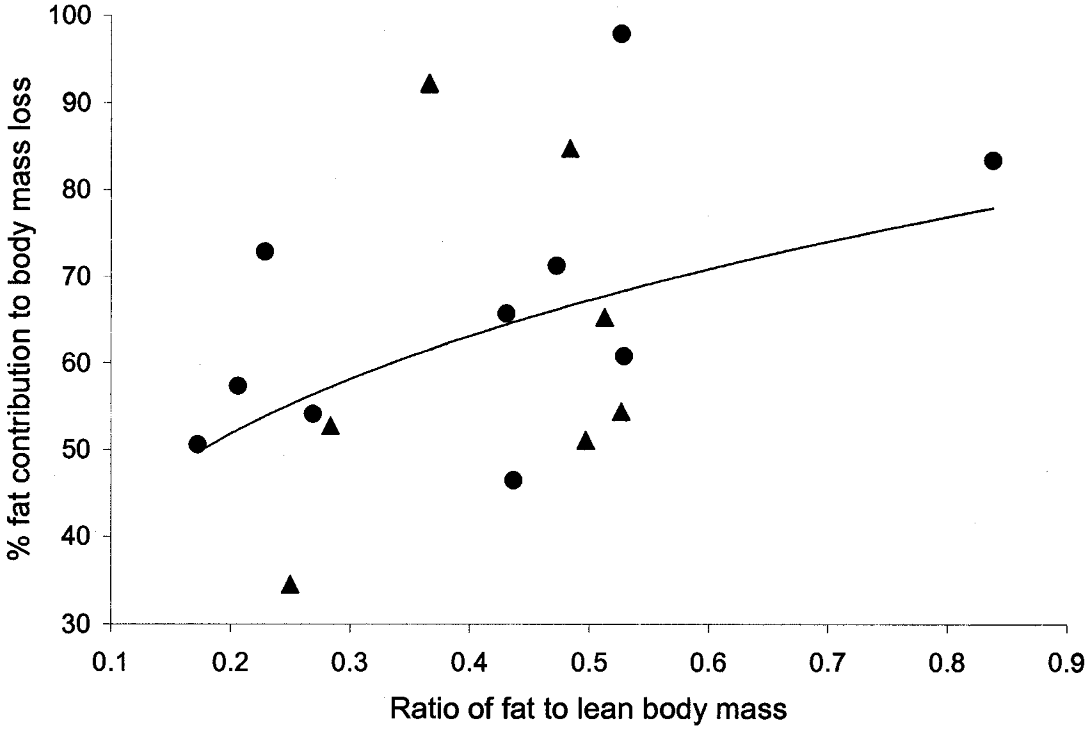

Fig. 1.6 Relationship between relative amount of fat in autumn (fat/lean body mass) and the contribution of fat to body mass loss during hibernation for brown (triangles) and American black (circles) bears, southcentral Alaska, 1999-2000.

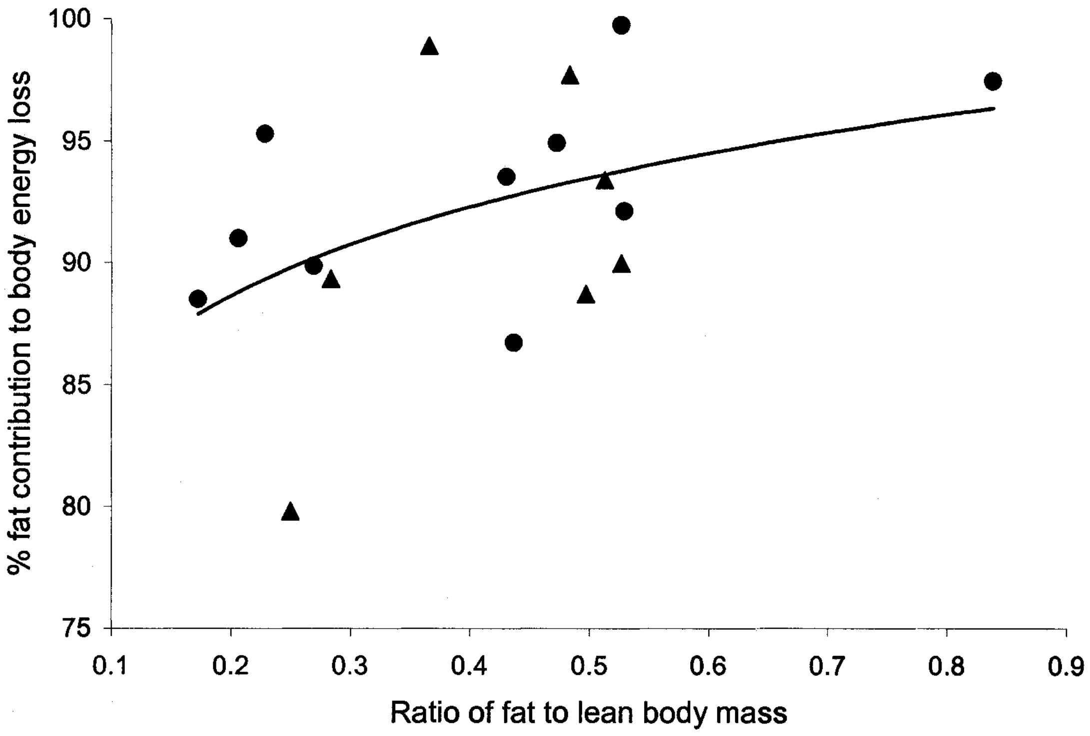

Fig. 1.7 Relationship between relative amount of fat in autumn (fat/lean body mass) and the contribution of fat to body energy loss during hibernation for brown (triangles) and American black (circles) bears, southcentral Alaska, 1999-2000.

POPULATION-LEVEL RESOURCE SELECTION BY SYMPATRIC BROWN AND AMERICAN BLACK BEARS

Abstract Distribution theory of habitat selection predicts that for two species living in sympatry, the subordinate species would be constrained from using the most suitable resources (e.g., habitat), resulting in its use of less suitable habitat and spatial segregation between species. I used negative binomial generalized linear mixed models to estimate seasonal population-level resource selection at two spatial resolutions for female brown bears (*Ursus arctos*) and American black bears (*U. americanus*) in southcentral Alaska during May-September 2000. Black bears selected areas occupied by brown bears during spring which may be related to spatially-restricted (i.e., restricted to low elevations) but dispersed availability of food. In contrast, black bears avoided areas used by brown bears during summer. Brown bears used narrower ranges of elevations during spring and summer, likely in part to access available food sources. Female brown bears also selected areas near salmon streams during summer, presumably to access spawning salmon. Use of dwarf shrub/herbaceous vegetation by black bears during summer appeared in response to high berry production and avoidance of areas containing brown bears that presumably had access to alternate highly-digestible food (i.e., salmon). Berries likely provided black bears a less nutritious, but adequate food source. I suggest that during summer, black bears were displaced by brown bears, resulting in their increased use of dwarf shrub/herbaceous vegetation. My data supports the despotic distribution model in that black bears appeared to be partially constrained from areas containing salmon, resulting in their use of areas containing less nutritious forage.

However, habitat attributes were more important in explaining black bear distribution than was brown bear presence. Spatial segregation of brown and American black bears apparently occurs when high-quality resources are spatially restricted and alternate resources are available to the subordinate species. This and previous work suggest that individual interactions between species can result in seasonal population-level responses.

Keywords American black bear · brown bear · habitat selection · interspecific competition · negative binomial · spatial segregation · *Ursus* spp.

Introduction

Habitat selection occurs at the individual level. Fretwell (1972) originated a theory and develop two models explaining habitat selection. The ideal free-distribution model suggests that habitat suitability is related inversely to the density of the species occupying that habitat. When animal density decreases suitability of the most suitable habitat to that of the second most suitable habitat, individuals will begin to occupy the second habitat. The ideal despotic-distribution model has application to species exhibiting territorial behavior (Fretwell 1972). In this model, aggressive behavior of individuals causes subordinate animals to occupy lower quality habitat. Extending this theory to two species implies the subordinate species may be constrained from using the most suitable habitat by the dominant species.

The geographic ranges of American black and brown bears apparently overlapped extensively in North America prior to European settlement (Herrero 1972). In Alaska, brown and black bears still currently coexist throughout much of the state (Kolenosky and Strathearn 1987; Jonkel 1987). The larger body size of brown bears provides a competitive advantage over black bears (Herrero 1978). Brown bears are considered the most important predator of black bears and may exclude black bears through interference competition, particularly if resources (e.g., food) of high value are patchy (McLellan 1993). Brown bears may displace black bears from high quality habitat (Shaffer 1971, Kendall 1984, Aune 1994); however, these studies did not use population inference. There are also occasional reports of predation on black bears by brown bears (Jonkel and Cowan 1971, Murie 1981, Ross et al. 1988, Mattson et al. 1992, Smith and Follmann 1993, Gunther et al. 2002). Under the ideal despotic-distribution model, black bears would be considered subordinate to brown bears and consequently displaced from areas used by brown bears through competition.

Where the two species coexist, black bears are more typically found in forest-dominated areas (Stirling and Derocher 1990, 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. McLellan (1993) suggested that coexistence can occur in forested areas with diverse and widely distributed food sources (e.g., ungulates, berries, salmon). Reported means of coexistence between brown and black bears include spatial separation (Aune 1994), temporal differences in activity (Shaffer 1971, MacHutchon et al. 1998, Holm et al. 1999), and use of different foods (Jacoby et al. 1999). Previous studies of sympatric brown and black bears most frequently have emphasized differences in habitat (resource) use to describe coexistence (Kasworm and Their 1990; Aune 1994; Holm et al. 1999). However, these studies did not explicitly assess population-level responses (Thomas et al. 2006).

There are four commonly accepted experimental designs for assessing resource selection (Erickson et al. 2001, Manly et al. 2002). Design I studies assess resource selection at the population level by comparing resource use to resource availability; availability is defined as a predetermined study area or the polygon including animal locations. Designs II and III use individuals as the units of replication and assess selection relative to habitat available within the study area and individual home range, respectively. Design IV studies employ paired use and availability measures where resource use is estimated multiple times. Advantages of using individual animals (designs II-IV) rather than individual locations (design I) as the unit of replication are now well established (Aebischer et al. 1993, Alldredge et al 1998, Thomas and Taylor 2006).

Logistic regression is likely the method used most frequently to estimate resource selection (Thomas and Taylor 2006). A disadvantage of this approach is that areas considered unused may actually be used but misclassified as unused because of low sampling frequency or animal detection rates of <1 (Johnson et al. 2006, MacKenzie

2006). Further, the binary (used/unused) response from logistic regression does not accommodate multiple observations of animals in the same location. Consequently, loss of information commonly occurs from telemetry studies that use this method. Other distributions (e.g., Poisson) used in general linear models or generalized linear mixed models can accommodate multiple animal observations from the same location and have been used to model resource selection (e.g., Millspaugh et al. 2006). In these situations, habitat attributes are derived from cells distributed randomly or systematically across the area of interest, and count data for individuals are estimated for each cell (Millspaugh et al. 2006, Thomas et al. 2006).

Attempts have been made to quantify population-level selection, including averaging parameter estimates across individuals and reporting the number of individuals with similar parameter coefficients (D'Eon 2003, Zielinski et al. 2004, Millspaugh et al 2006). The former approach will work if the number of locations is nearly the same for each animal. However, if the number of locations differs substantially among animals, population parameter estimates will be disproportionately influenced by animals with more locations. Including random effects can provide information on variation in resource selection among individuals and improve model performance (Gillies et al 2006, Thomas et al. 2006). Although random effects may not be of primary interest to managers, they can be used to assess resource selection of various animal cohorts (e.g., by sex or age class) within the overall model (Thomas et al. 2006).

I used population-level seasonal resource selection models employing a design II approach to assess spatial segregation and habitat use by brown and American black bears in southcentral Alaska. Initially, from the ideal despotic-distribution model I hypothesized avoidance of brown bears by black bears during all seasons. To provide a complimentary test for this hypothesis, I also modeled brown bear use relative to areas occupied by black bears. I then tested several hypotheses related to brown and black bear seasonal use of specific habitat attributes. I hypothesized seasonally bimodal use of elevation by brown bears (Waller and Mace 1997, McLellan and Hovey 2001, Nielsen et al. 2002). Specifically, I expected brown bears during spring to move from higher-elevation denning areas to access new growth of vegetation occurring at lower elevations (e.g., Mace and Waller 1997). I also hypothesized that brown bears would select habitats during spring that were used by moose for calving, particularly areas with tall shrubs including willow (*Salix* spp.) or alder (*Alnus* spp.) (Langley and Pletscher 1994, Bowyer et al. 1999). In late summer, I expected brown bears to move from low to high elevations prior to the onset of denning. Because of the importance of salmon to brown bears (Hilderbrand et al 1999*a*, Jacoby et al. 1999, Belant et al. 2006), I also hypothesized that in summer brown bears would use areas close to streams containing salmon. Because of the extensive use of salmon by brown bears (Hilderbrand et al. 1999, Jacoby et al. 1999, Belant et al. 2006), I did not consider brown bear use of vegetation types during summer.

As with brown bears, I hypothesized that black bears would select vegetation types in spring that contained new growth of vegetation (e.g., grasses, tree leaves), typical components of their diet during this time of year (Kolenosky and Strathearn 1987). I also hypothesized that black bears would exhibit unimodal use of mid-elevations during summer in response to vegetation types containing berries. I expected black bears to select the dwarf shrub/herbaceous habitat which contained crowberry (*Empetrum nigrum*) and blueberry (*Vaccinium* spp.); berries are typical items in black bear diets throughout much of their geographic range (Kolenosky and Strathearn 1987).

Materials and Methods

Study Area

The study was conducted during May-September 2000 in southcentral Alaska, bounded by the Alaska Range to the north, the Yentna River drainage to the west, the Chulitna River drainage on the east, and 62°15' latitude forming the southern boundary. This area included the southeastern portion of Denali National Park and Preserve and Denali State Park. Elevations ranged from about 130-1,650 m. Several medium-sized glacial-fed rivers traversed the study area. Lower elevations were characterized by spruce (*Picea glauca* and *P. mariana*), poplar (*Populus* spp.), white birch (*Betula papyrifera*), and alder (*Alnus* spp.) with numerous wet meadows containing sedges and grasses. Mid elevations (about 400-800 m) contained shrub-dominated habitat including dwarf birch (*B. nana*) and willow (*Salix* spp.). With the exception of stream drainages which contained shrubs or small trees, elevations >800 m were dominated by tundra, exposed rocky slopes, and glaciers. Tree leaf-out at lower elevations began during mid-May; snowcover at lower elevations arrived from late September-early October.

Five species of Pacific salmon (*Oncorhynchus* spp.) occurred within the study area during spawning runs (Denali National Park and Preserve, unpubl. data), with about 47,000 individuals present during 2000 (Belant et al. 2006). The dominant ungulate was moose (*Alces alces*); estimated moose density during 2000 was 51 individuals/100 km^2 (Alaska Department of Fish and Game 2002). Caribou (*Rangifer tarandus*) and Dall's sheep (*Ovis dalli*) were not present in the study area. Dominant berry species included blueberry and crowberry. These species occurred primarily at mid-elevations; blueberry also occurred in low-density spruce woodlands at low elevations. Soapberry (*Sheperdia canadensis*) occurred along gravel bars of major rivers. Other vegetation common in bear diets included horsetail (*Equisetum* sp.), devil's club (*Oplopanax horridum*), ferns, grasses, and sedges (Kolenosky and Strathearn 1987).

Animal Capture and Telemetry

I captured bears during mid May, late June, and late September 2000. I defined spring as May-June and summer as July-September. Captures in May occurred as brown bears were emerging from dens; black bears had emerged during late April. Captures in June occurred just before the onset of salmon spawning runs in the study area. Captures in September occurred before den entrance although many bears had begun moving to higher elevations where most dens were ultimately located.

Bears observed initially by spotters in fixed-wing aircraft were captured using immobilizing darts fired from a helicopter (Taylor et al. 1989). I monitored body temperature, respiration, and heart rate of bears during handling procedures. Independent female bears ($\geq$4 and $\geq$5 years old for black and brown bears, respectively) were fitted with global positioning system (GPS) telemetry collars (Belant and Follmann 2002). GPS collars were programmed to attempt relocations at 60-min intervals and were retrieved during September captures to download data. Mean (standard deviation [SD]) percent of successful locations for these collared individuals was 75.9% (7.2) for black bears and 80.6% (7.7) for brown bears (Belant and Follmann 2002). All animal capture and handling procedures were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks.

Study Design and Resource Attributes

I analyzed telemetry data using a Design II approach which addresses study area-level selection with individual animals as the unit of replication (Manly et al. 2002, Thomas and Taylor 2006). This approach is appropriate for measuring population-level response to habitat features (Manly et al 2002, Thomas et al. 2006). The study area was defined by creating a 100% minimum convex polygon (MCP) around all bear relocations. I generated a 2-km^2 grid which comprised 1,484 cells that were within or intersected the MCP. I selected this resolution because preliminary analyses suggested this approximated the maximum number of cells that could be analyzed effectively. I similarly created a 4-km^2 grid consisting of 396 cells to estimate the effects of a coarser resolution on resource selection.

Because variation in seasonal habitat use by brown and black bears has been demonstrated (Beecham and Rohlman 1994, McLellan and Hovey 2001, McLoughlin et al. 2002), I initially calculated the number of locations of each bear in each cell during each season. Because I hypothesized black bear avoidance of brown bears *a priori*, I included the total number of brown bear locations in each cell by season as a continuous model term (BRBEAR) for respective black bear models. To compliment this hypothesis, I similarly included the number of black bear locations in each cell as a model term (BLBEAR) for respective brown bear models.

I used ArcGIS (Environmental Systems Research Institute, Redmond, California, USA) to extract habitat and bear location data. Vegetation was estimated from a landcover map developed from 1985 multi-spectral satellite imagery with 80-m resolution resampled to 50 m (Fitzpatrick-Lins et al. 1989). No catastrophic events (e.g., fire) occurred in the study area between image acquisition and this study.

In contrast to most resource selection studies that model the probability of use of vegetation classes (Fuller and Harrison 2005, Patten et al. 2005); I modeled the probability of use of discrete areas of land (Thomas et al. 2006). I initially determined the dominant vegetation type (VEG) in each grid cell using the zonal majority routine in ArcGIS. Vegetation classes defined for analyses included conifer forest, deciduous forest, tall shrub, dwarf shrub/herbaceous, sparse/non-vegetated, and snow/ice. Tall shrub vegetation consisted primarily of alder (*Alnus* spp.) with some willow (*Salix* spp.). The dwarf shrub/herbaceous vegetation class include dwarf birch, crowberry, and blueberry.

I incorporated a GIS layer of elevation (U.S. Geological Survey 30-m Digital Elevation Models [www.edc.usgs.gov/geodata]) in analyses. I defined the model term ELEV as the median elevation for each grid cell. I also included a quadratic term for elevation ($ELEV^2$) because of my hypothesized nonlinear use of elevations by bears.

I calculated the distance from the center of each grid cell to the nearest river or stream documented to contain salmon (DISSTREAM). I conducted aerial surveys for spawning salmon during September 2000. Salmon were assumed to occur in portions of rivers if they were observed in reaches or tributaries upstream. I also reviewed unpublished data from previous salmon surveys (Alaska Department of Fish and Game, unpubl. files; Denali National Park and Preserve, unpubl. files) to aid in determining salmon distribution. This information was integrated with existing GIS hydrographic data (Denali National Park and Preserve, unpubl. data) to develop the layer of streams containing spawning salmon.

Model Selection

To estimate population-level selection, I used three generalized linear mixed models (GLMM) with the habitat and seasonal bear location data and compared their performance to select the model most appropriate for final analyses of resource selection. Models were developed using PROC GLIMMIX (SAS Institute 2005) and included: 1) negative binomial model with individual animal random effects, 2) negative binomial model with fixed effects, and 3) Poisson model with overdispersion. As animals may vary in selection of habitat features, models with random effects consider animals as heterogenous units in which each animal is represented as a block. In contrast, models with fixed effects do not consider heterogeneity among individual animals. I used the Poisson model with overdispersion because the number of observations for a given cell often exceeds the variability predicted by the Poisson distribution (Zhang et al. 2006).

For each of these models, I used the I × J random matrix **Y**, with each Y_{ij} cell containing the number of locations represented by row (i) for an individual bear in column (j). I then modeled Y_{ij} using the expected number of locations in row i by animal j as:

$$E(Y_{ij}) = \mu_{ij},$$

for $i = 1, 2, 3, \ldots, I$ and $j = 1, 2, 3, \ldots, J$.

For the negative binomial models, I assumed that $Y_{ij} \sim NB(\mu_{ij}, k)$ with the probability mass function:

$$f(y_{ij} \mid \mu_{ij}, k) = \frac{\Gamma(y_{ij} + K)}{\Gamma(k)\Gamma(y_{ij} + 1)} \left(\frac{k}{\mu_{ij} + k}\right)^{k} \left(1 - \frac{k}{\mu_{ij} + k}\right)^{y_{ij}},$$

Where μ_{ij} is the mean and $k > 0$ is the scale parameter. This distribution has the variance:

$$V(Y_{ij}) = \mu_{ij} + \mu_{ij}^{2}/k,$$

which is greater than the mean μ_{ij} when k is positive.

The resulting loglinear negative binomial model with individual animal random effects would be:

$$\ln(\mu_{ij}) = \mathbf{x}_i \cdot \boldsymbol{\beta}_j,$$

where $\mathbf{x}_i$ is the vector of explanatory variables characterizing cell i and $\boldsymbol{\beta}_j$ is a multi-dimensional parameter vector for animal j. I assumed a multivariate normal distribution of $\boldsymbol{\beta}$ for this model. The negative binomial model without individual animal random effects (j) would be written as:

$$\ln(\mu_i) = \mathbf{x}_i \cdot \boldsymbol{\beta},$$

The loglinear Poisson model without random effects generally can be described similarly to the negative binomial model without random effects. Data overdispersion in the Poisson model often occurs when fitting this distribution with animal count data (Millspaugh et al. 2006). To address overdispersion, and to increase model flexibility (Agresti 1990), I accounted for overdispersion by assuming that only a functional relationship existed between the mean and variance which can be described as:

$$V(Y_i) = \phi\mu_i$$

for some constant ϕ. Overdispersion is present in the Poisson model when $\phi > 1$ (Agresti 1990:457).

I selected model terms specific to my original hypotheses to estimate seasonal resource selection by each species. For brown bears, I used the model terms VEG, ELEV, $ELEV^2$, and BLBEAR during spring and DISSTREAM, ELEV, $ELEV^2$, and BLBEAR during summer. For black bears, I used the model terms VEG and BRBEAR during spring and VEG, ELEV, $ELEV^2$ and BRBEAR during summer. For each set of models, I included the global model which contained all terms relevant to my hypotheses and the null (intercept only) model. I standardized continuous variables before analyses to avoid possible variation in scale (Thomas et al. 2006). For models that included VEG, I used tall shrub as the standard vegetation type against which other vegetation types were compared (Manly et al. 2002).

I compared performance of each set of models using Akaike Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 1998). Models with AIC_c scores within 2 of the best-supported model ($AIC_c = 0$) were considered similarly supported (Burnham and Anderson 1988). I also calculated averaged model Akaike weights (*w*), which measure model support and model selection uncertainty (Burnham and Anderson 1988). Finally, I used model averaging of selected models to estimate model parameters and decrease model selection uncertainty (Burnham and Anderson 1998).

Results

I captured 11 independent female brown and 13 independent female black bears during May 2000 that were used for analyses during spring. An additional 5 and 3 independent female black and brown bears, respectively, were captured during June 2000. Thus, 16 individuals of each species were used for analyses during summer. The number of locations per individual averaged 736 (SD = 178) for brown bears and 523 (SD = 178) for black bears during spring, and 1,306 (SD = 498) for brown bears and 1,080 (SD = 320) for black bears in summer. Overall, I obtained 53,605 locations (Fig. 1), including 8,097 brown bear and 6,793 black bear locations during spring (May-June) and 20,903 brown bear and 17,272 black bear locations during summer (July-September).

The percentage of 2-km^2 cells with zero bear locations was 81.4% and 90.0% for brown and black bears, respectively, during spring and 66.8% and 80.9%, respectively, in summer. At the 4-km^2 resolution, percentage of zero cells was 74.5% and 86.1% of cells for brown and black bears, respectively, in spring, and 57.1% and 72.7% respectively, during summer.

In my initial assessment using global models at both spatial resolutions, I did not consistently obtain model convergence using Poisson with overdispersion (7 of 8 models converged) or the negative binomial with random effects (2 of 8 models converged). In contrast, the negative binomial model without random effects consistently met model convergence criteria (8 of 8 models converged). Thus, for final analyses I used the negative binomial model without individual animal random effects to assess population-level resource selection by brown and black bears at the two spatial resolutions (2 km^2 and 4 km^2).

Resource Selection

The best supported models for brown bears in spring included elevation and black bear use (Table 2.1). Brown bears selected areas used by black bears at both spatial resolutions (Table 2.2). Nonlinear use of elevation during spring occurred at both spatial resolutions with greatest relative use between 400-800 m and 900-1000 m (Fig. 2).

In contrast to spring, brown bears did not use areas occupied by black bears at either spatial resolution during summer. Nonlinear elevation use also occurred during summer, with about 30% of brown bear use occurring at 200-300 m elevation. Brown bears selected areas nearest salmon streams at both resolutions during summer (Table 2.2); 73% and 94% of brown bear use were in areas <300 m and <500 m of salmon streams, respectively.

The most parsimonious models for black bears during spring were those which included vegetation or vegetation and intensity of brown bear use (Table 2.1). Overall, black bears selected deciduous and dwarf shrub vegetation and avoided other vegetation types relative to tall shrub at the 2 km^2 resolution (Table 2.2). Black bears selected deciduous and sparse/non-vegetated areas at the 4-km^2 resolution. As evidenced by positive parameter estimate coefficients, black bears demonstrated overall selection for the same as brown bears at both spatial resolutions.

During summer, the best supported models for black bear at the 2-km^2 resolution included vegetation, elevation, and intensity of brown bear use (Table 2.1). Relative to tall shrub, black bears selected dwarf shrub/herbaceous and avoided all other vegetation types (Table 2.2). Black bears disproportionately used elevations <500m and 600-700 m. Black bears did not demonstrate selection for vegetation types but did exhibit nonlinear use of elevation at the 4 km^2 resolution. In contrast to spring, black bears demonstrated avoidance of areas with brown bear use during summer at both resolutions.

Discussion

Resource Selection

I observed population-level spatial avoidance of black bears and brown bears during summer, supporting the extension of the ideal despotic distribution model. Brown bears are occasional predators of black bears (Mattson et al. 1992, Smith and Follmann 1993, Gunther et al. 2002) and may exclude black bears through interference competition (McLellan 1993). On one occasion in summer I observed a female black bear with two dependent young about 10 m above ground in a poplar tree where the bears had apparently retreated from a brown bear standing at the base. It has also been suggested that brown bears can displace black bears from areas of mutual use (Shaffer 1971, Kendall 1984, Aune 1994). As only female bears were monitored in this study, my estimates of black bear avoidance of brown bears are likely conservative. Female brown bears are subordinate to male brown bears (Wielgus and Bunnell 1994, 1995; McLellan 2005), suggesting that male brown bears also would probably dominate in interactions with black bears. Also, success of relocating black bears using GPS collars in forested areas may have been lower than relocation success in other habitats (Rempel et al. 1995), resulting in conservative estimates of use in conifer habitat. Consequent inflated use of other habitats that may have been occupied by brown bears would have reduced my estimates of spatial avoidance. Brown and black bears interact at the individual level; results from this and previous studies suggest that these interactions can cause a population-level response as evidenced by spatial avoidance by black bears occurring at multiple scales.

When available, salmon is probably the most important dietary item for brown and black bears (Hilderbrand et al. 1999*a*, Jacoby et al. 1999). Jacoby et al. (1999) reported that salmon represented 53% of the assimilated diet in an allopatric black bear population from the Kenai Peninsula, Alaska. Salmon comprised 58% and 25% of the respective assimilated diets for brown and black bears in my study area during summer 2000 (Belant et al. 2006). I suggest that in accord with the ideal despotic distribution model, black bears were subordinate to brown bears and consequently displaced in part from areas with available salmon, through some form of interference competition.

In contrast to my prediction, I observed black bears selecting areas occupied by brown bears during spring. Observed mutual selection may also be related to limited availability of food, which is common for bears during spring (Noyce and Garshelis 1998). Comparatively poor relocation success in conifer forests (e.g., Rempel et al. 1995) may in part explain this observed selection. Salmon availability was undoubtedly limited during spring, and primary food sources likely consisted of new growth of vegetation, berries from the previous year, or moose calves (Atwell et al. 1980, Schwartz and Franzmann 1991, Mace and Jonkel 1986). As vegetation growth in mountainous areas initially occurs later than at lower elevations during spring, food availability may have been spatially restricted to lower elevations. Additionally, new plant growth would likely be dispersed throughout these areas. Although black bears selected areas used by brown bears, presumably to forage, available food may have been sufficiently dispersed such that black bears could not be excluded by brown bears. Black bear avoidance of brown bears in spring may occur at finer spatial resolutions than investigated here.

Brown bears in this study demonstrated nonlinear use of elevation during spring and summer. Brown bears in mountainous areas frequently exhibit elevation shifts, primarily in response to seasonal variation in food and den site selection (Servheen and Klaver 1983, Miller 1990, Mace and Waller 1997, McLellan and Hovey 2001). Selection of specific elevations during summer was likely related in part to salmon vulnerability to predation.

As I predicted, brown bears exhibited selection for salmon streams during summer at both spatial resolutions. The importance of salmon in brown bear diets has been described previously (Hilderbrand et al. 1999*a*, Jacoby et al. 1999). In this study area, salmon represented almost 60% of the assimilated diet in brown bears during summer 2000 (Belant et al. 2006), so I was confident brown bears were using streams containing salmon. Thus, I expected brown bears to select areas in close proximity to streams during summer to have access to available salmon. Female brown bears were estimated closer to salmon streams in this study than estimates reported by Hilderbrand et al. (1999*b*), who suggested that brown bears on the Kenai Peninsula, Alaska, spent about 50% of their time within 500 m, and up to 80% of time within 1 km, of streams containing salmon.

Black bears preferred the deciduous and dwarf shrub/herbaceous vegetation types during spring. When available, black bears will eat the catkins and young leaves of aspens or poplars and birch (Kolenosky and Strathearn 1987), the dominant tree species in the deciduous vegetation type. Use of dwarf shrub/herbaceous areas may have been in response to new growth of vegetation or the presence of berries from the previous year.

As predicted, black bears preferred the dwarf shrub/herbaceous habitat during summer. In addition to spatial avoidance of brown bears, this was likely also a consequence of food availability. Crowberries were highly abundant in this habitat during summer 2000; several black bears were captured in this habitat during September with mouths and fur stained purple from this fruit. Plant material which included berries represented the majority of black bear diets during this period (Belant et al. 2006). Although plant materials are energetically less nutritious than meat (Pritchard and Robbins 1990), given their small body size compared to brown bears, black bears can gain a significant amount of body mass with a predominantly herbivorous diet (Welch et al. 1997).

GLMM Performance

The negative binomial model with fixed effects outperformed the Poisson model with overdispersion for my bear location data. The number of cells with zero counts of animals may have been large enough to cause the variance to exceed the mean expected use of cells. My use of an overdispersion parameter was also unsuccessful, suggesting a non-multiplicative functional relationship between the variance and mean existed (Agresti 1990). Others have suggested the negative binomial model as an alternative to Poisson for modeling animal count data (e.g. Kery et al. 2005, Millspaugh et al. 2006).

The negative binomial model with individual animals as random effects did not perform as well as the negative binomial model with fixed effects. Zhang et al. (2006) also reported that negative binomial models with random effects sometimes failed to converge. Model convergence is more likely when there are larger samples of individuals and comparatively greater numbers of cells with nonzero values. I believe there were adequate numbers of locations for individual bears to estimate resource selection; however, I had few total individuals (*n* = 11-16) of each species. Several authors have recommended ≥20 individuals with ≥50 independent locations for modeling population-level resource selection (Alldredge and Ratti 1986, Thomas et al. 2006).

Conclusions

I described the first effort to model spatial segregation and seasonal habitat selection of sympatric brown and American black bears using explicit population-level inference. My hypothesis of black bear avoidance of brown bears under the ideal despotic distribution model was rejected in part as areas used by black bears and brown bears were positively associated during spring. I surmise this was related to spatially-restricted (i.e., restricted to low elevations) but dispersed availability of food and the spatial resolution used to model resource selection. In contrast, the ideal despotic distribution model was supported by bear resource selection during summer, suggesting that black bears were displaced by brown bears from areas with spawning salmon, resulting in increased black bear use of the dwarf shrub/herbaceous vegetation class. That is, black bear access to salmon may have been restricted by brown bears, causing increased use of berries by black bears (Belant et al. 2006). Black bears appeared to be spatially constrained from areas containing seasonal resources of high nutritive value, resulting in their use of areas containing less suitable forage. Although spatial avoidance by black bears was demonstrated, habitat attributes appeared to more strongly influence each species' distribution. This work, in combination with previous individual-based observations, suggests that avoidance of brown bears by black bears can occur at multiple spatial and temporal scales and that individual interactions or avoidance of interactions influence population-level responses. Sympatry with finer-scale spatial segregation of brown and American black bears apparently occurs when desired resources are spatially restricted and alternate resources are available to the subordinate species.

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References

Aebischer NJ, Robertson PA, Kenward RE (1993) Compositional analyses of habitat use from animal radio-tracking data. Ecology 74:1313-1325

Agresti A (1990) Categorical data analysis. John Wiley & Sons, New York, New York

Alaska Department of Fish and Game (2002) Moose management report of survey-inventory activities 1 July 1999-30 June 2001. Project 1.0, Juneau, Alaska, USA

Alldredge JR, Thomas DL, McDonald LL (1998) Survey and comparison of methods for study of resource selection. J Agric Biol Environ Stat 3:327-253

Alldredge JR, Ratti JT (1986) Comparison of some statistical techniques for analysis of resource selection. J Wildl Manage 50:157-165

Atwell GC, Boone DL, Gustafson D, Berns VD (1980) Brown bear summer use of alpine habitat on the Kodiak National Wildlife Refuge. Int Conf Bear Res Manage 7:99-107

Aune KE (1994) Comparative ecology of black and grizzly bears on the Rocky Mountain Front, Montana. Int Conf Bear Res Manage 9:365-374

Beecham JJ, Rohlman J (1994) A shadow in the forest: Idaho's black bear. Univ Idaho Press, Moscow, Idaho

Belant JL, Follmann EH (2002) Sampling considerations for American black and brown bear home range and habitat use. Ursus 13:153-169

Belant JL, Kielland K, Follmann EH, Adams LG (2006) Interspecific resource partitioning in sympatric ursids. Ecol Appl 16:in press

Bowyer RT, Van Ballenberghe V, Kie JG, Maier JAK (1999) Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. J Mammal 80:1070-1083

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York

D'Eon RG (2003) Effects of a stationary GPS fix-rate bias on habitat selection analyses. J Wildl Manage 67:858-863

Erickson WP, McDonald TL, Gerow KG, Howlin S, Kern JW (2001) Statistical issues in resource selection studies with radio-marked animals. In: Millspaugh JJ, Marzluff

JM (eds) Radio tracking and animal populations, Academic, San Diego, California. pp 211-245

Fitzpatrick-Lins K, Droughty GF, Shasby M, Benjamin S (1989) Alaska interim land cover mapping program—final report, Open-File Rep 89-128, U.S. Geological Survey, Reston, Virginia, USA

Fretwell SD (1972) Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey

Fuller AK, Harrison DJ (2005) Influence of partial timber harvesting on American martens in north-central Maine. J Wildl Manage 69:710-722

Gillies CS, Hebblewhite M, Nielsen SE, Krawchuk MA, Aldridge CL, Frair JL, Saher DJ, Stevens CE, Jerde CL (2006) Application of random effects to the study of resource selection. J Anim Ecol 75:887-898

Gunther KA, Biel MJ, Anderson N, Waits L (2002) Probable grizzly bear predation on an American black bear in Yellowstone National Park. Ursus 13:372-374

Herrero S (1972) Aspects of evolution and adaptation in American black bears (*Ursus americanus* Pallus) and brown and grizzly bears (*Ursus arctos* Linne') of North America. Int Conf Bear Res Manage 2:221-231

Herrero S (1978) A comparison of some features of the evolution, ecology, and behavior of black and grizzly/brown bears. Carnivore 1:7-16

Hilderbrand GV, Hanley TA, Robbins CT, Schwartz CC (1999*b*) Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia 121:546-550

Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C (1999*a*) The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Can J Zool 77:132-138

Holm GW, Lindzey FG, Moody DS (1999) Interactions of sympatric black and grizzly bears in northwest Montana. Ursus 11:99-108

Jacoby ME, Hilderbrand GV, Servheen C, Schwartz CC, Arthur SM, Hanley TA, Robbins CT, Michener R (1999) Trophic relations of brown and black bears in several North American ecosystems. J Wildl Manage 63:921-929

Johnson CJ, Nielsen SE, Merrill EH, McDonald TL, Boyce MS (2006) Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. J Wildl Manage 70:347-357

Jonkel CJ (1984) Grizzlies and black bear interrelationships. Spec Rep 70, Border Grizzly Proj, University of Montana, Missoula

Jonkel CJ (1987) Brown bear. In: Novak M, Baker JA, Obbard ME, Malloch B (eds) Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, pp 457-473

Jonkel CJ, Cowan IM (1971) The black bear in the spruce-fir forest. Wildl Monogr 27:1-57

Kasworm W, Their TJ (1990) Cabinet-Yaak ecosystem grizzly bear and black bear research, 1989 progress report. US Fish Wildl Serv, Missoula, Montana

Kendall KC (1984) Grizzly bear population trend studies, Apgar Mountains, Glacier National Park—1983 Progress Report. US Dep Int, Natl Park Serv, Glacier Natl Park, Glacier, Montana

Kery M, Royle A, Schmid H (2005) Modeling avian abundance from replicated counts using binomial mixture models. Ecol Appl 15:1540-1461

Kolenosky GB, Strathearn SM (1987) Black bear. In: Novak M, Baker JA, Obbard ME, Malloch B (eds) Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, pp 443-454

Langley MA, Pletscher DH (1994) Calving areas of moose in northwestern Montana and southeastern British Columbia. Alces 30:127-135.

Mace RD, Jonkel CJ (1986) Local food habits of the grizzly bear in Montana. Int Conf Bear Res Manage 6:105-110

Mace RD, Waller JS (1997) Final report: grizzly bear ecology in the Swan Mountains, Montana. Montana Fish, Wildlife and Parks, Helena

MacKenzie DI (2006) Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. J Wildl Manage 70:367-374

MacHutchon AG, Himmer S, Davis H, Gallagher M (1998) Temporal and spatial activity patterns among coastal bear populations. Ursus 10:539-546

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer, New York

Mattson DJ, Knight RR, Blanchard BM (1992) Cannibalism and predation on black bears by grizzly bears in the Yellowstone ecosystem, 1975-1990. J Mamm 73:422-425

McLellan BN (1993) Competition between black and grizzly bears as a natural population regulating factor. Proceedings western black bear workshop 4:111-116

McLellan BN, Hovey FW (2001) Habitats selected by grizzly bears in a multiple use landscape. J Wildl Manage 65:92-99

McLellan BN (2005) Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. Ursus 16:141-156.

McLoughlin PD, Case RL, Gau RJ, Cluff HD, Mulders R, Messier F (2002) Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. Oecologia 132:102-108

Miller SD (1990) Denning ecology of brown bears in southcentral Alaska and comparisons with a sympatric black bear population. Int Conf Bear Res Manage 8:279-287

Miller SD, White GC, Sellers RA, Reynolds HV, Schoen JW, Titus K, Barnes VG, Smith RB, Nelson RR, Ballard WB, Schwartz CC (1997) Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. Wildl Monogr 133:1-55

Millspaugh JJ, Nielson RM, McDonald L, Marzluff JM, Gitzen RA, Rittenhouse CD, Hubbard MW, Sheriff SL (2006) Analysis of resource selection using utilization distributions. J Wildl Manage 70:384-395.

Murie A (1981) The grizzlies of Mount McKinley. US Natl Park Serv Sci Monogr Ser 14, Washington, DC, USA

Nielsen SE, Boyce MS, Stenhouse GB, Munro RHM (2002) Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. Ursus 13:45-56

Noyce KV, Garshelis DL (1998) Spring weight changes in black bears in north central Minnesota: the negative foraging period revisited. Ursus 10:521-531

Patten MA, Wolfe DH, Shochat E, Sherrod SK (2005) Effects of microhabitat and microclimate selection on adult survivorship of the lesser prairie-chicken. J Wildl Manage 69:1270-1278

Pritchard GT, Robbins CT (1990) Digestive and metabolic efficiencies of grizzly and black bears. Can J Zool 68:1645-1651

Rempel RS, Rodgers AR, Abraham KF (1995) Performance of a GPS animal location system under boreal forest canopy. J Wildl Manage 7:235-242

Ross PI, Hornbeck GE, Horejsi BL (1988) Late denning black bears killed by grizzly bear. J Mammal 69:818-820

SAS Institute (2005) The GLIMMIX procedure. SAS Institute, Cary, North Carolina

Schwartz CC, Franzmann AW (1991) Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildl Monogr 113:1-58

Servheen C, Klaver R (1983) Grizzly bear dens and denning activity in the Mission and Rattlesnake Mountains: Montana. Int Conf Bear Res Manage 5:201-207

Shaffer SC (1971) Some ecological relationships of grizzly bears and black bears of the Apgar Mountains in Glacier National Park, Montana. MS thesis, University of Montana, Missoula

Smith ME, Follmann EH (1993) Grizzly bear, *Ursus arctos*, predation of a denned adult black bear, *U. americanus*. Can Field-Nat 107:97-99

Stirling I, Derocher AE (1990) Factors affecting the evolution and behavioral ecology of the modern bears. Int Conf Bear Res Manage 8:189-204

Taylor WP, Reynolds III HV, Ballard WB (1989) Immobilization of grizzly bears with tiletamine hydrochloride and zolazepam hydrochloride. J Wildl Manage 53:978-981

Thomas DL, Johnson D, Griffith DB (2006) A Bayesian random effects discrete-choice model for resource selection: population-level selection inference. J Wildl Manage 70:404-412

Thomas DL, Taylor EJ (2006) Study designs and tests for comparing resource use and availability II. J Wildl Manage 70:324-336

Waller JS, Mace, RD (1997) Grizzly bear habitat selection in the Swan Mountains, Montana. J Wildl Manage 61:1032-1039

Welch CA, Keay J, Kendall KC, Robbins CT (1997) Constraints on frugivory by bears. Ecology 78:1105-1119.

Wielgus RB, Bunnell FL (1994) Sexual segregation and female grizzly bear avoidance of males. J Wildl Manage 58:405-413

Wielgus RB, Bunnell FL (1995) Tests of hypothesis for sexual segregation in grizzly bears. J Wildl Manage 59:552-560

Zhang Y, Thomas DL, Griffith B (2006) Poisson and negative binomial models for analyzing habitat selection data. Univ Alaska Fairbanks, unpubl rep, Fairbanks, Alaska

Zielinski WJ, Truex RL, Schmidt GA, Schlexer FV, Schmidt KN, Barrett RH (2004) Resting habitat selection by fishers in California. J Wildl Manage 68:4`75-492

Table 2.1 Model-fitting results for resource selection of 2 km^2 and 4 km^2 cells by brown and American black bears in southcentral Alaska during spring (May-June) and summer (July-September) 2000. Models are compared according to number of parameters (*K*), Akaike's Information Criterion corrected for sample size ($\mathrm{AIC_c}$), the difference in $\mathrm{AIC_c}$ from best-fitting model ($\Delta\mathrm{AIC_c}$), model weight (*w*), and model rank.

				2 km^2 cells				4 km^2 cells			
Species	Season	Model[a]	*K*	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	*w*	Rank	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	*w*	Rank
Brown	Spring	ELEV, ELEV^2	4	5836.2	0.0	0.56	1	2564.3	0.0	0.51	1
		ELEV, ELEV^2, BLBEAR	5	5837.6	1.4	0.28	2	2564.5	0.2	0.46	2
		VEG, ELEV, ELEV^2	9	5840.6	3.4	0.10	3	2571.6	7.3	0.01	3
		VEG, ELEV, ELEV^2, BLBEAR	10	5841.7	4.5	0.06	4	2571.8	7.5	0.01	4
		VEG	7	5860.2	24.0	<0.01	5	2575.4	11.1	<0.01	6
		VEG, BLBEAR	8	5861.6	25.4	<0.01	6	2576.4	12.1	<0.01	8

Table 2.1 (Continued)

Species	Season	Model[a]	*K*
Brown	Spring	NULL	2
		BLBEAR	3
	Summer	DISSTREAM, ELEV, ELEV^2	5
		DISSTREAM, ELEV, ELEV^2, BLBEAR	6
		DISSTREAM	3
		DISSTREAM, BLBEAR	4
		ELEV, ELEV^2, BLBEAR	5

2 km² cells				4 km² cells			
AIC$_c$	ΔAIC$_c$	*W*	Rank	AIC$_c$	ΔAIC$_c$	*W*	Rank
5865.0	28.8	<0.01	7	2574.6	10.3	<0.01	5
5866.9	30.7	<0.01	8	2576.2	11.9	<0.01	7
11849.3	0.0	0.65	1	5067.5	0.0	0.69	1
11850.5	1.2	0.35	2	5069.2	1.7	0.30	2
11872.1	22.8	<0.01	3	5076.7	9.2	0.01	3
11873.4	24.1	<0.01	4	5078.1	10.6	<0.01	4
11925.2	75.9	<0.01	5	5107.8	40.3	<0.01	6

Table 2.1 (Continued)

Species	Season	Model[a]	K
Brown	Summer	ELEV, ELEV^2	4
		NULL	2
		BLBEAR	3
Black	Spring	VEG	7
		VEG, BRBEAR	8
		NULL	2
		BRBEAR	3
	Summer	VEG, ELEV, ELEV^2	9
		VEG, ELEV, ELEV^2, BRBEAR	10
		ELEV, ELEV^2	4

2 km^2 cells				4 km^2 cells			
AIC$_c$	ΔAIC$_c$	*W*	Rank	AIC$_c$	ΔAIC$_c$	*W*	Rank
11926.8	77.5	<0.01	6	5106.4	38.9	<0.01	5
11987.5	138.2	<0.01	7	5125.8	58.3	<0.01	7
11987.6	138.3	<0.01	8	5127.5	60.0	<0.01	8
3050.3	0.0	0.73	1	1270.7	0.0	0.63	1
3052.3	2.0	0.27	2	1272.6	1.9	0.24	2
3094.8	44.5	<0.01	3	1274.7	4.0	0.09	3
3096.4	46.4	<0.01	4	1276.4	5.7	0.04	4
6607.9	0.0	0.54	1	2909.2	2.9	0.12	3
6608.2	0.3	0.46	2	2910.7	4.4	0.06	4
6619.1	11.2	<0.01	3	2906.3	0.0	0.52	1

Table 2.1 (Continued)

				2 km^2 cells				4 km^2 cells			
Species	Season	Model[a]	K	AIC_c	ΔAIC_c	W	Rank	AIC_c	ΔAIC_c	W	Rank
Black	Summer	ELEV, ELEV^2, BRBEAR	5	6619.5	11.6	<0.01	4	2907.8	1.5	0.25	2
		VEG	7	6622.8	14.9	<0.01	5	2912.0	5.7	0.3	5
		VEG, BRBEAR	8	6622.8	14.9	<0.01	5	2913.4	7.2	0.1	6
		NULL	2	6651.4	43.5	<0.01	6	2918.0	11.7	<0.01	7
		BRBEAR	3	6652.4	44.5	<0.01	7	2919.8	13.5	<0.01	8

[a] Model terms are elevation (ELEV), quadratic elevation (ELEV^2), distance to nearest stream containing salmon (DISSTREAM), dominant vegetation type (VEG), intensity of brown bear use (BRBEAR), and intercept only (NULL).

Table 2.2 Model averaged population-level habitat selection parameter estimates for brown and American black bears using 2 km^2 and 4 km^2 cells, southcentral Alaska, during spring (May-June) and summer (July-September) 2000. All models with ΔAIC_c scores ≤ 2 are included.

			2 km^2 cells				4 km^2 cells			
					95% confidence Limit				95% confidence Limit	
Species	Season[a]	Model term	Parameter estimate	Standard error	Upper	Lower	Parameter estimate	Standard error	Upper	Lower
Brown	Spring	ELEV	2.219	0.214	1.458	3.123	2.917	0.626	1.581	4.444
		ELEV^2	-2.723	0.257	-3.633	-0.591	-3.419	0.704	-5.039	-1.800
		BLBEAR	0.019	0.003	-0.034	0.073	0.104	0.018	-0.072	0.281
	Summer	ELEV	2.289	0.201	1.410	3.168	2.738	0.535	1.311	4.164
		ELEV^2	-1.865	0.520	-3.708	-1.686	-3.063	0.635	-4.618	-1.509
		DISSTREAM	-1.865	0.090	-2.249	-1.507	-2.665	0.184	-3.330	-2.203
		BLBEAR	-0.032	0.032	-0.100	0.036	-0.030	0.007	-0.123	0.060

Table 2.2 (Continued).

			2 km² cells				4 km² cells			
					95% confidence level				95% confidence level	
Species	Season	Model term	Parameter estimate	Standard error	Upper	Lower	Parameter estimate	Standard error	Upper	Lower
Black	Spring	Conifer	-3.205	0.539	-4.393	-2.019	-4.178	2.659	-7.160	-1.197
		Deciduous	0.195	0.050	0.069	0.494	0.635	0.001	0.410	0.704
		Dwarf shrub/ herbaceous	0.701	0.371	0.090	1.485	-3.006	1.435	-5.195	-0.818
		Sparse/non-vegetated	-2.655	0.095	-3.151	-1.290	1.465	0.003	1.371	1.557
		Snow/Ice	-3.701	0.384	-4.081	-1.634	-0.152	0.063	-0.613	0.307
		BRBEAR	0.009	0.004	-0.120	0.139	0.018	0.022	-0.124	0.159
Black	Summer	Conifer	-4.669	1.086	-6.711	-2.626				

Table 2.2 (Continued).

			2 km^2 cells				4 km^2 cells			
					95% confidence level				95% confidence level	
Species	Season	Model term	Parameter estimate	Standard error	Upper	Lower	Parameter estimate	Standard error	Upper	Lower
Black	Summer	Deciduous	-0.264	0.204	-1.141	-0.021				
		Dwarf shrub/ Herbaceous	1.256	0.698	-0.384	2.893				
		Sparse/non-vegetated	-0.520	0.177	-1.344	0.304				
		Snow/Ice	-1.637	0.400	-2.872	-0.002				
		ELEV	-0.075	0.489	-1.353	1.382	0.784	0.595	-0.541	2.108
		ELEV^2	-1.040	0.473	-2.389	0.308	-1.545	0.716	-3.182	-0.339
		BRBEAR	-0.087	0.005	-0.213	0.038	-0.041	0.012	-0.147	0.067

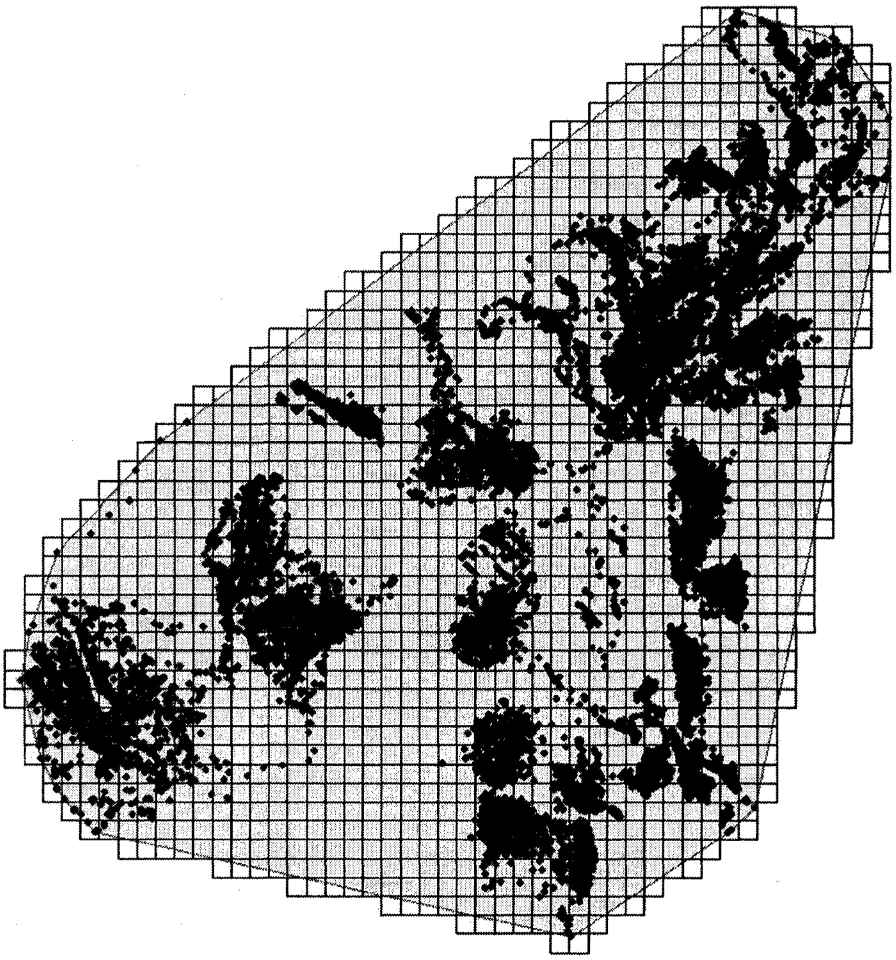

Fig. 2.1 Distribution of radio telemetry locations of bears (brown and American black) during May-September 2000, southcentral Alaska. Grid size is 2 km^2; solid line is 100% minimum convex polygon of all bear locations.

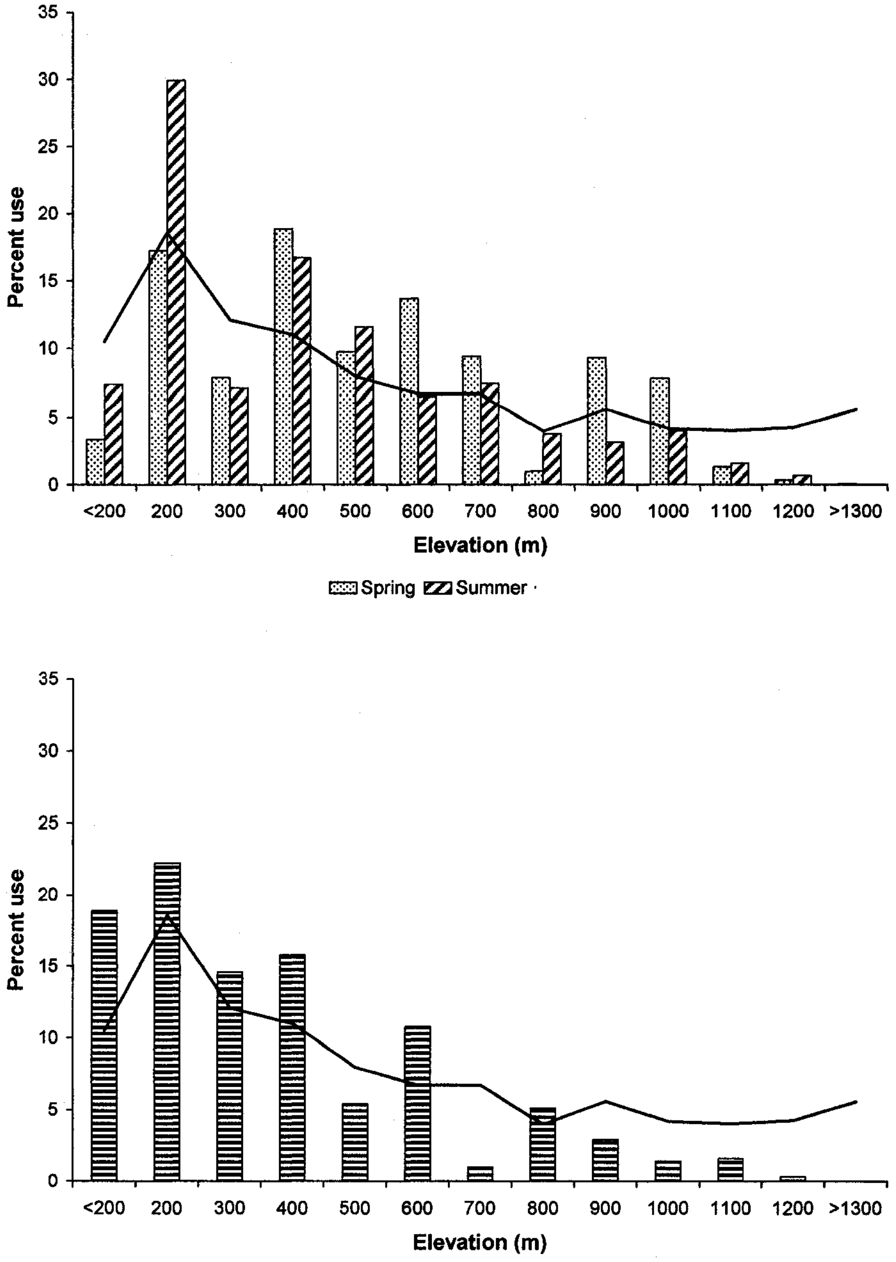

Fig. 2.2 Percent use of elevation classes by brown bears (top panel) during spring (May-June) and summer (July-September), and by black bears (bottom panel) during summer, 2000, southcentral Alaska. Solid line represents percent of cells by elevation classes within study area.

SAMPLING CONSIDERATIONS FOR AMERICAN BLACK AND BROWN BEAR HOME RANGE AND HABITAT USE[1]

Abstract: We deployed 72 collars with global positioning system (GPS) receivers on female brown bears (*Ursus arctos*) and black bears (*U. americanus*) in southcentral Alaska during 1998-2000 to evaluate collar performance and to estimate home range and habitat use. Overall, 67% of relocation attempts were successful (range = 10-93%). Most frequent causes for unsuccessful relocation attempts were inadequate number of satellites available and GPS antenna failure. There were differences ($P < 0.05$) in proportion of successful relocations by time of day, with lower success during 0800-1359 and 1800-0159 h. The proportion of successful relocations also decreased ($P < 0.05$) across half-month intervals. Using minimum convex polygon (MCP) and fixed kernel simulations for 6 individuals of each species, We estimated that >40 locations were typically required to estimate May-September home ranges and that >40 and >50 locations were typically necessary to estimate spring (late May-Jun) and summer (Jul-late Sep) home ranges. Precision of both models increased with sample size. More locations were generally required to describe the total area used by a bear (MCP method) than the utilization distribution using the fixed kernel method. For each bear, within-year habitat use differed ($P < 0.05$) seasonally. Within-season habitat use differed ($P < 0.05$) among

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[1] Belant, J. L., and E. H. Follmann. 2002. Sampling considerations for American black and brown bear home range and habitat use. Ursus 13:299-315.

individuals for each species. Furthermore, diurnal (0700-1859 h) and nocturnal (1900-0659 h) seasonal habitat use differed ($P < 0.05$) in 13% and 42% of all cases for black and brown bears, respectively. Acquiring adequate relocations to estimate home range and habitat use with conventional VHF telemetry may be prohibitive, particularly in remote areas. Potential biases from obtaining locations during only a portion of the 24-h period should also be considered. Analyses and interpretation of habitat data derived from studies with too few locations should be made with caution. Future investigators of black and brown bear home range and habitat use need to consider sampling designs seriously to ensure that data collected meets study objectives.

Key words: Alaska, black bear, brown bear, fixed kernel, global positioning system, habitat use, home range, minimum convex polygon, radio telemetry, *Ursus americanus*, *Ursus arctos*.

INTRODUCTION

Radio telemetry has been used in studies of free-ranging wildlife for almost 40 years (Rodgers 2001). The most frequent type of wildlife radio telemetry or radio tracking involves very high frequency (VHF) transmitters attached to animals from which investigators use a receiver to obtain the transmitted frequency to estimate animal locations. Although initial cost of VHF telemetry equipment is comparatively low, costs increase rapidly as the number of animals and locations required to meet study objectives increase. Wildlife studies in remote or extensive study areas frequently require aerial radio telemetry, which can increase costs even more. Furthermore, because of logistic and economic constraints, certain types of studies (e.g., fine-grained habitat use) may not be practical. In the early 1980s, substantial advances in technology resulted in the development of satellite telemetry systems, most notably Argos- and GPS-based systems (Fancy et al.1988, Harris et al. 1990, Tomkiewicz 1996, Rodgers 2001). Depending on study objectives and location, these systems offer considerable potential for reducing logistical problems.

Various methods for estimating animal home ranges have been developed, beginning with the minimum area polygon (Mohr 1947). Despite several shortcomings of this technique (White and Garrot 1990, Seaman et al. 1999), the minimum area polygon remains one of the most common home range estimators in use. Numerous nonparametric home range estimators and associated software have since been developed including the harmonic mean, fourier series, bivariate and modified bivariate normal model 95% ellipse estimator, and adaptive and fixed kernel methods (Jenrich and Turner 1969, Koeppl et al. 1975, Dixon and Chapman 1980, Anderson 1982, Worton 1987, Seaman et al. 1999). Of the nonparametric methods available, the fixed kernel has been recently considered the most suitable for estimating animal home ranges (Worton 1995, Seaman et al. 1998, 1999).

Although telemetry technology and home range modeling techniques have received considerable attention, less emphasis has been placed on determining the number of locations necessary to define with precision the home range of animals. Several authors have recently conducted simulation analyses using theoretical or empirical datasets (Worton 1995, Hansteen et al. 1997, Seaman and Powell 1996, Seaman et al. 1999). Little information, however, is available for determining the number of locations necessary to define the home ranges of bears. Arthur and Schwartz (2001) modeled brown bear home ranges on the Kenai Peninsula, Alaska, using MCP and kernel methods. Through simulation using empirical data, these authors found that >60 (MCP) and >80 (fixed kernel) locations were required to obtain precise (coefficient of variation [CV] < 0.50) estimates of home ranges during June-September. We are not aware of simulations with empirical data used to estimate the number of locations necessary to define black bear annual home ranges or seasonal home ranges of either species.

Estimating the use of space within the home range of an animal is critical for assessing habitat use. Several previous bear habitat use studies have employed what has been termed a Design I study (Thomas and Taylor 1990, Manly et al. 1993). In Design I studies, habitat is measured at the population level and individuals are not considered. The potential shortcomings of this design have been described (White and Garrott 1990, Manly et al. 1993, Otis and White 1999). Other bear habitat use studies have employed Design II and III studies which consider the individual animal and are preferable for habitat use analysis (Manly et al. 1993, Otis and White 1999). Advantages include using design-based rather than model-based inferences, employing techniques at the individual rather than population level, and ability to examine possible differences among cohorts (Manly et al. 1993).

In addition to an improved understanding of basic experimental design, considerable effort has been focused recently on improving analytical models for habitat use studies (Aebischer et al 1993, Manly et al. 1993, Cherry 1996, Gautestad et al. 1998). With the exception of seasonal habitat use (e.g., Costello and Sage 1994, Waller and Mace 1997, McLellan and Hovey 2001), however, little attention has focused on potential temporal effects on habitat use. Schooley (1994) documented problems associated with pooling habitat use data across years for black bears. This author found that preferred habitats differed among years and that combining data from multiple years masked these preferences. Beyer and Haufler (1994) documented variation in daily sampling period for determining habitat use of elk (*Cervus elaphus*), noting significant differences between day and night habitat use. Thus, substantial temporal variation in habitat use may exist that is not typically incorporated in studies of bear habitat use. In addition, the number of locations required to define adequately home ranges to provide estimates of habitat availability appear to be considered infrequently.

Our goal was to determine sampling requirements necessary to describe black and brown bear home range and habitat use. Specific objectives were 1) to evaluate the efficacy of GPS collars on black and brown bears, 2) to determine the precision of annual and seasonal home ranges using MCP and fixed kernel methods, and 3) to determine if habitat use differs between seasons and by time of day.

STUDY AREA

The study was conducted during May-Sep, 1998-2000 in southcentral 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 about 180-1,650 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 (about 400-800 m) contained shrub-dominated habitat including dwarf birch (*B. glandulosa*) and willow (*Salix* spp.). With the exception of stream drainages which contained shrubs or small trees, elevations >800 m were dominated by tundra, exposed rock slopes, and glaciers.

METHODS

Capture and Handling

Bears were captured opportunistically by aerially searching mountain slopes, river drainages, and open meadows and tundra. Bears initially observed by spotters in fixed-wing aircraft were captured using immobilizing darts fired from a helicopter (Taylor et al. 1989). Bears were immobilized with a combination of equal parts tolazoline and zolazopam (Telazol®, Fort Dodge Laboratories, Inc., Fort Dodge, Iowa). We monitored body temperature, respiration, and heart rate of bears during handling procedures. Female bears were then fitted with a GPS store-on-board collar with VHF transmitter which weighed 1.7 kg. After handling, bears were typically left at the capture site to recover from the immobilant and were checked by aircraft 1-2 days later to assess recovery. Capture and handling procedures were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee.

We deployed 72 GPS collars, typically during May. Collars (*n* = 12, 24, and 36 in 1998-2000, respectively) were distributed equally between independent females of each species each year. Memory was not restored on 11 collars refurbished for use in 1999; these collars were excluded from analyses. We attempted to retrieve all collars at the end of each field season and sent them to the manufacturer to download location data and refurbish collars for use in subsequent years.

Telemetry System

We used first- and second-generation GPS store on board collars (Telonics Inc., Mesa, Arizona). Characteristics of these collars have been described previously (Tomkiewicz 1996, Schwartz and Arthur 1999). Depending on the model and year, these collars were programmed to attempt locations of animals at 5 h, 95 min, or 60 min intervals beginning 5 or 10 May at 0000 h Greenwich Mean Time. GEN I collars recorded fix number, date, time, latitude, longitude, and general cause of unsuccessful location. GEN II collars included information contained in GEN I collars in addition to whether the location was 2D or 3D, horizontal dilution of precision, and satellites used to obtain locations.

GPS Collar Performance

We summarized causes of failure to obtain successful locations for each bear as recorded by the GPS receivers. To avoid potential bias between individual bears, only bears for which we obtained locations throughout an entire field season were used in analyses (*n* = 20 black bears and 12 brown bears).

To compare percent of successful locations during the 24-h period, we divided data into 12 2-hr intervals beginning at 0000 h. To assess temporal trends, data were divided into approximate half-month intervals beginning with late May. Location data for each bear were arcsine transformed before performing repeated measures analysis of variance (SAS Institute, Inc. 1988). Statistical significance for these and all other analyses was established as $P < 0.050$.

Home Range

We selected 6 individuals of each species that received GPS collars during 2000 for home range analyses. Home ranges were modeled using the MCP and fixed kernel methods (Hayne 1949, Seaman and Powell 1996). We chose the MCP method because of its frequent use in estimating home ranges and the fixed kernel method with least-squares cross validation because of its improved performance over other nonparametric estimators (Worton 1995, Seaman et al. 1999). We modeled MCP ranges using a modification of a previously developed computer program (White and Garrott 1990, Arthur and Schwartz 2001). Fixed kernel ranges were modeled using the software program KERNELHR (Seaman et al. 1998). In addition to modeling overall home ranges (late May-late Sep), we also modeled spring (late May-Jun) and summer (Jul-late Sep) home ranges for each bear. We defined fixed kernel home range estimates as the 95% use distributions estimated from bear locations.

For each bear-season, we randomly selected telemetry locations (without replacement) in increments of 10 locations. To approximate field conditions more closely using standard VHF telemetry techniques, selection of locations was restricted such that not more than 1 location/day was used for each random draw. Locations within a day were also selected at random. We used a maximum of 40 locations for spring, 80 for summer, and 100 for spring and summer combined. Because of the relative low number of locations obtained for 1 black bear, a maximum of 70 locations was used for this individual during summer. We obtained 1,000 random draws for each combination of bear, season, and sample size. Thus, for each bear, we conducted 4,000 simulations during spring, 8,000 during summer, and 10,000 combined home range estimates using MCP and fixed kernel methods. We plotted mean home range size against sample size for each bear-season combination. To assess precision in home range estimates and make direct comparisons among home range methods, species, and seasons, we plotted the CV against sample size. We arbitrarily chose a CV of <0.20 to represent reasonable precision in home range estimates (Boulanger and White 1990, Otis and White 1999).

Home range size generally changes asymptotically with sample size for both the MCP (area increases) and fixed kernel (area decreases) methods (White and Garrott 1990, Seaman et al. 1999). At present, no standardized technique exists for determining when the number of locations obtained adequately represents the home range of an animal. Metzgar and Sheldon (1974) used regression techniques to determine the asymptote of change in area with increasing sample size to estimate home range. Other authors (e.g., Van Dyke et al. 1995, Seaman et al. 1999) have used the approximate asymptote of area as an indication of suitable sample size. Odum and Kuenzler (1955) suggested that a sample size in which each additional location resulted in an area increase of ≤1% was adequate. We plotted percent change in mean home range size relative to the next lower sample size for each combination of method, bear, and season. We then approximated the suggestion of Odum and Kuenzler (1955) as described by Arthur and Schwartz (2001) in which the sample size was considered adequate to describe the home range when each additional 10-location increment resulted in a home range change of ≤10%.

Habitat Use

Habitat use was determined from a landcover map developed from 1985 multi-spectral satellite imagery with 80-m resolution resampled to 50 m (Fitzpatrick-Lins, K., G. F. Droughty, M. Shasby, and S. Benjamin. 1989. Alaska interim land cover mapping program – final report. Open-File Report 89-128, U.S. Geological Survey, Reston, Virginia, USA). ARC/INFO (ARC/INFO. 1998. Environmental Systems Research Institute, Redmond, California, USA.) was used to extract habitat use data from imported bear location data. No catastrophic events (e.g., fire) occurred in the study area between image acquisition and this study. Habitats defined for analyses included conifer forest (overstory >66% conifer) deciduous forest (overstory >66% deciduous), mixed forest (overstory <66% conifer or deciduous), shrub, tundra, and sparse/non-vegetated.

We compared seasonal habitat use for individual bears during each year. In addition, we determined whether habitat use differed among individuals within each species by season each year. For additional habitat use analyses, we defined diurnal as

0700-1859 and nocturnal as 1900-0659 to distribute the number of locations approximately equally between periods and because the diurnal period generally approximated the time period used in previous radio-telemetry studies of bear habitat use conducted during daylight hours. Day and night time periods were not designed to reflect the amount of daylight in southcentral Alaska, which exceeded the defined diurnal period during the study.

To ensure sample sizes were large enough to avoid violating analytical assumptions (Zar 1984, White and Garrot 1990), we analyzed habitat use only for bears with ≥150 locations/season. We used Chi-square statistics (SAS Institute, Inc. 1988) to compare habitat use between seasons and time periods for each bear and within each season among individuals by species.

RESULTS

GPS Collar Performance

Overall, 67% of relocation attempts were successful (range = 10-93%). Most frequent causes for unsuccessful relocation attempts were inadequate number of satellites available and GPS antenna failure (Table 3.1). During 1998-1999, GPS antenna failure was apparently a result of the GPS antenna separating from the canister. This problem was particularly evident with grizzly bears; for example, in 1998, virtually no locations were obtained for 5 of 6 grizzly bears after June. The manufacturer consequently modified the GPS antenna which resolved the problem for the 2000 field season. The overall increase in percent successful locations from 1998-2000 was largely a consequence of correcting this problem. Thus, we believe that data collected during 2000 reflected actual collar performance.

Percent of successful location attempts differed among 2-hr intervals for both species ($F = 33.37$; 11,330 df; $P < 0.001$; Fig. 3.1). Fewer locations were obtained for black bears than brown bears from 0800-1359 ($F = 9.88$; 11,330 df; $P < 0.001$). Percent of successful location attempts for black bears was lower from 0800-1359 h than during the rest of the day. For brown bears, percent of successful relocations was lower during 1000-1359 h and 1800-0159 h.

There was a general decline overall in percent of successful locations across half-month intervals ($F = 29.82$; 7,210 df; $P < 0.001$, Fig. 3.2) for both species. There was also an interaction of location success and species ($F = 6.30$; 7,210 df; $P < 0.001$), with percent of successful locations declining at a greater rate for brown bears than black bears.

Home Range

MCP home ranges for both species typically reached an asymptote as sample sizes increased (Figs. 3.3-3.4). An exception was black bear 9952, whose summer and combined home ranges did not clearly reach an asymptote after 80 and 100 locations, respectively. In contrast, black and brown bear fixed kernel home ranges consistently decreased in area as sample sizes increased (Figs. 3.3-3.4). The only notable exception was black bear 0079, whose spring home range area continued to decrease at a similar rate through 40 locations.

Initial MCP home range areas were usually smaller than fixed kernel home ranges but were ultimately larger as sample sizes increased (Figs. 3.3-3.4). For black bears during spring, MCP home ranges generally became larger than fixed kernel home ranges between 20-30 locations (Fig. 3.3). However, the summer and combined home ranges of two black bears did not converge until 80 locations were modeled. Brown bear MCP and fixed kernel home ranges typically converged at 10-30 locations (Fig. 3.4).

Differences in MCP and fixed kernel home ranges were considerable for both species in all seasons. Black bear spring, summer, and combined MCP home ranges were as much as 5 times greater than were the same home ranges using fixed kernel (Fig. 3.3). Variation for brown bears was even greater, with spring, summer, and combined MCP home ranges as much as 17 times greater than were fixed kernel home ranges (Fig. 3.4).

Precision of home range estimates varied considerably between species and seasons (Figs. 3.5-3.6). Coefficients of variation were typically lower for MCP home ranges than fixed kernel home ranges of comparable sample size (Table 3.2). Similarly, CV for MCP home ranges stabilized with fewer locations than did CV for fixed kernel home ranges. Variability among fixed kernel estimates within a season was greater than MCP estimates for both species.

Black bear MCP home ranges during spring, summer, and combined were generally of adequate precision ($CV < 0.20$) between 20-30, 20-40, and 20-50 locations, respectively (Fig. 3.5, Table 3.2). The exception was black bear 9952, which required >70 locations during summer for CV to be <0.20. The CV for this individual's combined

MCP home range was 0.23 for 100 locations. Variability of black bear fixed kernel home ranges during spring remained high, with CVs of 0.33-1.06 at 40 locations. Precise estimates of combined black bear home ranges generally required >80 locations, with 3 individuals requiring >100 locations.

Fewer than 40 locations were needed typically for spring and summer brown bear MCP home ranges to have a CV < 0.20 (Fig. 3.6, Table 3.2). The exception was an individual which required >60 locations for the combined home range. In contrast, variability of 5 of 6 brown bear spring fixed kernel home ranges was >0.20 at 40 locations. Variability was high (CV >0.32) for 4 and 5 brown bear summer and combined home ranges using 80 locations. In fact, 5 of 6 brown bear combined home ranges using the fixed kernel method were imprecise (CV > 0.31) with 100 locations.

More than 40 locations were required for 4 black bears during spring to have a reduction in MCP home range area of <1%/location (Fig. 3.7). For a similar rate of area reduction in summer and combined MCP home ranges, 3 black bears required >30 locations, 2 required >40 locations, and 1 required >70 locations. Number of locations required for fixed kernel home range estimates was even greater. More than 40 locations were necessary for 5 of 6 spring black bear home ranges. In summer, 4 black bears required >40 locations and for combined home ranges, >40 locations were needed for 3 individuals.

More than 40 locations were required for 3 brown bears during spring to have a reduction in MCP home range area of <1%/location (Fig. 3.8). Similarly, 5 brown bears required >30 locations during summer and 3 brown bears required >40 locations for combined MCP home ranges. Using fixed kernel, all 6 bears required >40 locations for home range estimates during spring, summer, and combined seasons. For summer and combined home range estimates, 3 and 2 individuals, respectively, needed >70 locations.

Habitat Use

In all cases, spring and summer habitat use differed for individual black and brown bears ($x^2 = 14.99$-781.67, df = 4-5, $P \leq 0.010$). In addition, seasonal habitat use differed ($x^2 = 292.71$–$3{,}482.91$; df = 20-75; $P < 0.001$) among individuals within each species during each year (e.g., Fig. 3.9).

Several individuals of both species exhibited differences ($P < 0.050$) between diurnal and nocturnal habitat use (Table 3.3). For black bears, day and night habitat use differed ($P < 0.050$) in 11% and 14% of instances during spring and summer, respectively. For brown bears, day and night habitat use differed ($P < 0.050$) in 29% and 56% of instances during spring and summer, respectively. Diurnal and nocturnal seasonal habitat use differed ($P < 0.050$) in 13% and 42% of all cases for black and brown bears, respectively (e.g., Fig. 3.10).

DISCUSSION

GPS Collar Performance

Vegetation may have affected GPS collar performance in this study, percent of successful locations declined temporally for both species, with highest rates obtained during May-early July. Similarly, Schwartz and Arthur (1999) documented a temporal decline in successful locations obtained for brown bears in the Kenai Peninsula, Alaska. These authors concluded that GPS performance was largely unaffected by vegetation;

however, increased vegetative closure was inversely associated with fix rate. Although temporal variation was not assessed, vegetation also was determined to have a significant effect overall on successful location attempts of black bears and moose (*Alces alces*) (Rempel et al. 1995, Moen et al. 1996, Obbard et al. 1998). The decrease in number of locations obtained in this study may have resulted in part from a general increase in vegetative cover as summer progressed.

Although location acquisition rates declined temporally for both species, the rate of decline was greater for brown bears. This decline coincided with salmon spawning runs which began in July (summer) each year. At this time, brown bears typically moved to lower elevation riparian areas containing denser overstory vegetation to feed on salmon. Black bears moved less extensively and did not make comparable movements. Thus, the greater temporal reduction in successful locations for brown bears was likely influenced by major shifts in habitat use.

The lower number of successful locations observed during parts of the 24-hr period may be attributed to bear behavior. For example, bears moving into dense cover or lying down during a fix acquisition attempt would preclude successful locations. Similar to this study, Obbard et al. (1998) documented variability in successful location attempts for black bears by time of day, with fewer locations generally obtained during the afternoon and early morning. Lower success of locations obtained for brown bears in this study corresponds reasonably well with observed resting periods for grizzly bears in Denali National Park north of the Alaska Range (Stelmock and Dean 1986).

Home Range and Habitat Use

Although home ranges of some bears in this study were adequately described with as few as 30 locations, home ranges for the 'population' of bears were not defined during some seasons until ≥80 locations were obtained. For seasonal home ranges, this represented obtaining >1 location/day. More locations were necessary to define home ranges with adequate precision (CV <0.20). The minimum number of locations recommended previously for kernel home range analyses (≥30 or ≥50; Seaman et al. 1999) appear too few for defining black and brown bear home ranges, at least in this study area. For fixed kernel analyses, we recommend obtaining ≥80 locations to describe black and brown bear annual home ranges. For annual home ranges using MCP, we recommend using 60-90 locations.

Based on study objectives and definition of home range used, either MCP or fixed kernel may be employed for home range analyses. The MCP is useful for estimating the total area used by an individual, and has been used to evaluate home range overlap (Horner and Powell 1990, Wertz et al. 2001). In contrast, kernel methods provide a density estimate of the area used by an individual (White and Garrott 1990, Seaman et al. 1999) and are more suitable for resource selection studies.

Seaman et al. (1999) recognized that estimates along the periphery of home ranges are unreliable relative to estimates of core areas. Outer portions of the home range often contribute substantially to the total area yet the least amount of data are available to support these estimates. This appears to have a greater influence on MCP home ranges than kernel home ranges. Seaman et al. (1999) recommended that future studies place greater emphasis on core areas for home range and habitat selection analyses. Additional research with simulated and empirical data is required to assess the effects of sampling intensity on accuracy and precision of core areas within home ranges. Sample size and model used has been demonstrated to affect home range (Seaman et al. 1999, Arthur and Schwartz 2001, this study); similar effects may exist for core areas within home ranges.

Autocorrelation, or dependence of radio telemetry locations, often has been reported as a problem for home range and habitat use analyses (Swihart and Slade 1985, Litvaitis et al. 1994). Conversely, other authors have stated that autocorrelation typically will not be problematic, provided habitat use is defined at the individual level and data collection for home range analyses is unbiased during the period of interest (Swihart and Slade 1997, Otis and White 1999). Using Schoener's index t^2/r^2 (Schoener 1981, Swihart and Slade 1985) on black bears in North Carolina, Powell (1987) determined that it may not be possible to obtain enough statistically independent locations to estimate home ranges. Although we did not determine independence of locations, if Powell's (1987) estimates of the time interval for independence between locations were valid for this study, it would be difficult or impossible to determine home ranges on a seasonal or annual level. We believe that bear movements within a home range are not independent, that movements are in part a result of previous movements and experience. Although data for individual bears in this study were not independent, because data were collected systematically throughout defined intervals, we do not believe that autocorrelation of data is of concern (see Swihart and Slade 1997, Otis and White 1999).

A suitable number of locations was obtained in this study using GPS collars to assess habitat use at the individual level. Using location estimates as the sampling unit among individuals in a population to determine habitat use is a form of pseudoreplication (Otis and White 1999). These authors, among others (e.g., White and Garrott 1990, Thomas and Taylor 1990, Manly et al. 1993), have recommended that the individual animal be used as the unit of replication. Multiple techniques are available to define habitat use for a given population using the individual animal (Johnson 1980, Alldredge and Ratti 1986, 1990, Aebischer et al. 1993). Manly et al. (1993) and Otis and White (1999) described advantages of using individuals as the unit of replication.

It is often difficult to monitor enough individuals to have high power to detect differences in home range or habitat use (see Arthur and Schwartz 2001). Statisticians (e.g., Zar 1984) have demonstrated that the number of individuals represented is of greater importance than is the number of locations obtained for each individual. Otis and White (1999) further stated that GPS collars could enhance this problem because their greater cost may result in researchers buying fewer units and thus monitor fewer individuals. We support Otis and White (1999) in that both the number of locations obtained/individual and total number of individuals monitored is critical for assessing habitat use for a population. Too few individuals monitored will not adequately reflect the population; similarly, too few locations/individual will not represent the individual which in turn cannot represent the population. Ensuring that enough locations are obtained define the home range, whether seasonal or annual, will reduce error and provide better estimates of habitat use.

Otis and White (1999) mentioned the need to theoretically address the effects of variable numbers of locations obtained among individuals on habitat use. Indeed, in this study the number of locations varied by several hundred which could result in biased assessments of habitat use among bears. One solution would be to standardize the number of locations used among bears. A second method would be to standardize the precision among home range estimates. A third means to potentially reduce this problem is to use locations only to define the relative area used by each bear, for example, using the fixed kernel method to define individual 95% and 50% contours. In this case, habitat selection could be assessed by comparing habitat within the 50% contour ('preferred') to habitat within the 95% contour ('available'). This form of analyses may also aid in reducing the potential adverse effects of vegetative closure on fix rate. It should be recognized that heterogeneity of habitat (e.g., patch size and juxtaposition) could affect derived selection indices in this analyses. Using bears as the unit of replication would provide equal weight among individuals, further reducing this potential bias.

We reviewed 32 articles on black and brown bear habitat use published in the *Journal of Wildlife Management* (1977-2000) and from proceedings of *The International Conference on Bear Research and Management* (1977-1994) and *Ursus* (1998) to assess timing of data collection. A majority (79%) of these studies reported collecting habitat data only during the diurnal period or did not provide adequate detail to determine the timing of data collection. We presumed that the majority of studies that did not report the timing of collection obtained habitat use information collected during the day only. This study illustrates the importance of sampling habitat use based on the entire 24-h period.

For example, diurnal sampling of black bear habitat suggested higher than expected use of shrub habitat, whereas sampling at night revealed the relative importance of sparsely-vegetated habitat (Fig. 3.10). Similarly, diurnal brown bear habitat use was predominantly deciduous forest, whereas night sampling revealed almost equal use of shrub habitat.

In many portions of their range, brown and black bears have been reported as being primarily diurnal or crepuscular (Amstrup and Beecham 1976, Lindzey and Meslow 1977, Garshelis and Pelton, 1980, Bjarvall and Sandegren 1987, Mace and Waller 1997). In addition to the relative ease and convenience of collecting data during the day, this may explain why a majority of studies of bear habitat use were conducted during the diurnal period. However, many of the above-mentioned studies reported that bears were also active at night. Furthermore, that several studies have documented extensive diurnal or crepuscular activity does not imply that bears under some circumstances or in portions of their range cannot be at least as active during night as during the day. For example, Ayres et al. (1986) reported that black bears in Sequoia National Park that relied in part on food from campgrounds were active primarily during night whereas bears that relied on natural foods were primarily crepuscular. Brown bears have also been reported to be highly active at night (Pearson 1975, Roth 1983, Roth and Huber 1986, Stelmock and Dean 1986). Activity patterns and levels of activity can vary among cohorts (e.g., subadults, adult females with young), seasons, and even individual bears (Roth 1983, Roth and Huber 1986, Stelmock and Dean 1986, Gunther 1991, Mace and Waller 1997). Thus, habitat use studies should conduct initial assessments of bear activity patterns before establishing timing of location estimates.

MANAGEMENT AND RESEARCH IMPLICATIONS

Use of GPS collars offers several advantages over conventional VHF transmitters or other telemetry systems including collection of data during inclement weather, greater frequency of locations, reduction of human error, and increased cost effectiveness for multi-year studies (Schwartz and Arthur 1999). Accuracy of locations using satellite telemetry systems has been enhanced recently due to disablement of selective availability (Hulbert and French 2001). Satellite and GPS telemetry now provide biologists greater opportunity to collect data over 24 hours (Rodgers et al. 1996, Craighead 1998, Obbard et al. 1998). For home range and habitat studies in remote or large geographic areas, GPS or another satellite-based system may be the only practical alternative.

Because of differences in habitat use observed in this study, pooling location data for bears within or across seasons is not recommended. Pooling seasonal data could mask habitat selection, as has been demonstrated with between-year habitat selection for black bears (Schooley 1994). As diurnal and nocturnal habitat use can also differ for bears, inferences from data collected during only part of the 24-hr period cannot be extrapolated to the entire 24-hour period *a priori*. In our simplistic example, managers considering only daytime (0700-1859 h) brown bear habitat use may have decided to reduce human development in shrub and sparsely-vegetated areas whereas if 24-hour data had been available, greater emphasis may have been placed on protecting shrub habitat. Thus, management recommendations based on data collected during part of the 24-hour period could be misleading or even detrimental to affected populations. Timing of sampling and the potential limitations of habitat use data should be explicitly stated prior to formulating decisions.

We believe that additional integration of home range and habitat use methods is necessary to understand resource selection of bears, as well as other species. Incorporating appropriate sampling efforts relative to species' activity patterns and daily and seasonal use of resources is essential to define home ranges and associated habitat selection. Analyses and interpretation of habitat data derived from studies where habitat use was not a primary objective (i.e., too few locations) should be made with caution. Future studies need to collect enough locations to ensure reasonable estimates of home range and habitat use. Having adequate numbers of locations to analytically define home range or habitat use does not in itself mean data are unbiased. Additional research understanding apparent biases of canopy cover and bear behavior on location acquisition rates are needed to ensure accuracy of data. Future investigations of black and brown bear home range and habitat use must seriously consider sampling designs to ensure that data collected meets study objectives.

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K. Stahlnecker, and K. Wilson provided field and/or office assistance. J. (S.) Hamilton, J. Larrivee, H. McMahan, M. Meekin, and P. Walters were instrumental in safe and effective capture of study animals. P. A. Owen provided considerable assistance in all aspects of this project. S. Arthur kindly provided programming language for random location generation and MCP calculations; J. Paynter extracted habitat data from GIS themes. L. Adams, P. Barboza, K. Kielland, and R. Powell provided comments on earlier drafts of this manuscript. Funding for this study was provided by Denali National Park and Preserve, National Park Service Fee Demonstration Program, National Park Service Challenge Cost Share Program, and donations from Canon USA, Inc. through the National Park Foundation.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

Alldredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 50:157-165.

Amstrup, S. C., and J. Beecham. 1976. Activity patterns of radio-collared bears in Idaho. Journal of Wildlife Management 40:340-348.

Anderson, D. J. 1982. The home range: a new nonparametric estimation technique. Ecology 63:103-112.

Arthur, S. M., and C. C. Schwartz. 2001. Effects of sample size on accuracy and precision of brown bear home range models. Ursus 11:in press.

Ayres, L. A., L. S. Chow, and D. M. Graber. 1986. Black bear activity patterns and human induced modifications in Sequoia National Park. International Conference on Bear Research and Management 6:151-154.

Beyer, D. E., Jr., and J. B. Haufler. 1994. Diurnal versus 24-hour sampling of habitat use. Journal of Wildlife Management. 58:178-180.

Bjarvall, A, and F. Sandegren. 1987. Early experiences with the first radio-marked brown bears in Sweden. International Conference on Bear Research and Management 7:9-12.

Boulanger, J. G., and G. C. White. 1990. A comparison of home range estimators using Monte Carlo simulation. Journal of Wildlife Management 54:310-315.

Cherry, S. 1996. A comparison of confidence interval methods for habitat use-availability studies. Journal of Wildlife Management 60:653-658.

Costello, C. M. and R. W. Sage, Jr. 1994. Predicting black bear habitat selection from food abundance under 3 forest management systems. International Conference on Bear Research and Management 9:375-387.

Craighead, D. J. 1998. An integrated satellite technique to evaluate grizzly bear habitat use. International Conference on Bear Research and Management 10:187-201.

Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

Fancy, S. G., L. F. Pank, D. C. Douglas, C. H. Curby, G. W. Garner, S. C. Amstrup, and W. L. Regelin. 1988. Satellite telemetry: a new tool for wildlife research and management. U.S. Fish and Wildlife Service Resource Publication 172.

Garshelis, D. L., and M. R. Pelton. 1980. Activity of black bears in the Great Smoky Mountains National Park. Journal of Mammalogy 61:8-9.

Gautestad, A. O., I. Mysterud, and M. R. Pelton. 1998. Complex movement and scale-free habitat use: testing the multi-scaled home-range model on black bear telemetry data. Ursus 10:219-234.

Gunther, K. A. 1991. Visitor impact on grizzly bear activity in Pelican Valley, Yellowstone National Park. International Conference on Bear Research and Management 8:73-78.

Hansteen, T. L., H. P. Andreassen, and R. A. Ims. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. Journal of Wildlife Management 61:280-290.

Harris, R. B., S. G. Fancy, D. C. Douglas, G. W. Garner, T. R. McCabe, and L. F. Pank. 1990. Tracking wildlife by satellite: current systems and performance. U.S. Fish and Wildlife Service Technical Report 30.

Hayne, D. W. 1949. Calculation of home range size. Journal of Mammalogy 30:1-18.

Horner, M. A., and R. A. Powell. 1990. Internal structure of home ranges of black bears and analyses of home-range overlap. Journal of Mammalogy 71:402-410.

Hulbert, I. A. R., and J. French. 2001. The accuracy of GPS for wildlife telemetry and habitat mapping. Journal of Applied Ecology 38:869-878.

Jenrich, R. I., and F. B. Turner. 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22:227-237.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Koeppl, J. W., N. A. Slade, and R. S. Hoffmann. 1975. A bivariate home range model with possible application to ethological data analysis. Journal of Mammalogy 56:81-90.

Lindzey, F. G., and E. C. Meslow. 1977. Population characteristics of black bears on an island in Washington. Journal of Wildlife Management 41:408-412.

Litvaitis, J. A. K. Titus, and E. M. Anderson. 1994. Measuring vertebrate use of terrestrial habitats and foods. Pages 254-270 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

Mace, R. D., and J. S. Waller. 1997. Final report: grizzly bear ecology in the Swan Mountains. Montana Fish, Wildlife, and Parks, Helena, Montana, USA.

Manly, B., L. McDonald, and D. Thomas. 1993. Resource selection by animals. Chapman and Hall, New York, New York, USA.

McLellan, B. N., and F. W. Hovey. 2001. Habitats selected by grizzly bears in a multiple use landscape. Journal of Wildlife Management 65:92-99.

Metzgar, L. H., and A. L. Sheldon. 1973. An index of home range size. Journal of Wildlife Management 38:546-551.

Moen, R. A., J. Pastor, Y. Cohen, and C. C. Schwartz. 1996. Effects of moose movement and habitat use on GPS collar performance. Journal of Wildlife Management 60:659-668.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223-249.

Obbard, M. E., B. A. Pond, and A. Perera. 1998. Preliminary evaluation of GPS collars for analysis of habitat use and activity patterns of black bears. International Conference on Bear Research and Management 10:209-217.

Odum, E. P., and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. Auk 72:128-137.

Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63:1039-1044.

Pearson, A. M. 1975. The northern interior grizzly bear *Ursus arctos* L. Canadian Wildlife Service Report 34.

Powell, R. A. 1987. Black bear home range overlap in North Carolina and the concept of home range applied to black bears. International Conference on Bear Research and Management 7:235-242.

Rempel, R. S., A. R. Rodgers, and K. F. Abraham. 1995. Performance of a GPS animal location system under boreal forest canopy. Journal of Wildlife Management 59:543-551.

Rodgers, A. R. 2001. Recent telemetry technology. Pages __-__ *in* J. J. Millspaugh and J. M. Marzloff, editors. Radio-tracking and animal populations. Academic Press, San Diego, California, USA.

____________, R. S. Rempel, and K. A. Abraham. 1996. A GPS-based telemetry system. Wildlife Society Bulletin 24:559-566.

Roth, H. U. 1983. Diel activity of a remnant population of European brown bears. International Conference on Bear Research and Management 5:223-229.

____________, and D. Huber. 1986. Diel activity of brown bears in Plitvice Lakes National Park, Yugoslavia. International Conference on Bear Research and Management 6:177-181.

SAS Institute, Inc. 1988. SAS/STAT user's guide. Version 6.03. SAS Institute, Incorporated, Cary, North Carolina, USA.

Schoener, T. W. 1981. An empirically based estimate of home range. Theoretical Population Biology 20:281-325.

Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. Journal of Wildlife Management 58:367-374.

Schwartz, C. C., and S. M. Arthur. 1999. Radio-tracking large wilderness mammals: integration of GPS and ARGOS technology. Ursus 11:261-273.

Seaman, D. E., B. Griffith, and R. A. Powell. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26:95-100.

____________, J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.

____________, and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.

Stelmock, J. J., and F. C. Dean. 1986. Brown bear activity and habitat use, Denali National Park – 1980. International Conference on Bear Research and Management 6:155-167.

Swihart, R. K., and N. A. Slade. 1985. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49:1019-1025.

______, and ________ 1997. On testing for independence of animal movements. Journal of Agricultural, Biological, and Environmental Statistics 2:48-63.

Taylor, W. P., H. V. Reynolds, III, and W. B. Ballard. 1989. Immobilization of grizzly bears with tiletamine hydrochloride and zolazepam hydrochloride. Journal of Wildlife Management 53:978-981.

Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54:322-330.

Tomkiewicz, S. 1996. GPS applications for wildlife—a review. Telonics Quarterly 9(1):1-12.

Van Dyke, F. G., B. L. Probert, and G. M. Van Beek. 1995. Moose home range fidelity and core area characteristics. Alces 31:21-32.

Waller, J. S., and R. D. Mace. 1997. Grizzly bear habitat selection in the Swan Mountains, Montana. Journal of Wildlife Management 61:1032-1039.

Wertz, T. L., J. J. Akenson, M. G. Henjum, and E. L. Bull. 2001. Home range and dispersal patterns of subadult black bears in northeastern Oregon. Western Black Bear Workshop 7:93-100.

White, G. C., and R. A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York, New York, USA.

Worton, B. J. 1987. A review of models of home range for animal movement. Ecological Modeling 38:277-298.

_____________. 1995. Using monte carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794-800.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Table 3.1. Characteristics of GPS collar performance for black and brown bears, southcentral Alaska, May-September 1998-2000.

			Causes for location failure (mean % ± SD)	
Species	Year	Mean % (± SD) successful fixes	Too few satellites	No GPS time[a]
Black	1998	66.1 ± 7.5	20.5 ± 4.1	10.5 ± 8.0
	1999	61.4 ± 12.3	10.3 ± 5.4	25.5 ± 7.9
	2000	75.9 ± 7.2	17.2 ± 3.8	5.4 ± 4.5
	Combined	70.2 ± 10.9	15.8 ± 5.6	11.8 ± 10.6
Brown	1998	33.3 ± 17.8	15.7 ± 8.4	50.1 ± 25.7
	1999	44.1 ± 29.8	12.5 ± 6.7	43.2 ± 33.5
	2000	80.6 ± 7.7	13.4 ± 5.0	5.2 ± 3.2
	Combined	63.3 ± 26.3	13.7 ± 6.0	22.2 ± 27.4

[a] Includes GPS antenna failure (see results).

Table 3.2. Number of locations needed to define minimum convex polygon (MCP) and fixed kernel home range 'accuracy' (<1% mean change in area/additional location) and precision (CV <20%) for female black and brown bears, southcentral Alaska, 2000.

		Black bear		Brown bear	
Parameter	Season	MCP	Fixed kernel	MCP	Fixed kernel
Accuracy	Spring	≥40	30 - ≥40	≥40	>40
	Summer	40 - 80	40 – 70	40 – 60	50 - >80
	Combined	40 – 90	40 – 60	40 – 60	50 - 80
Precision	Spring	20 – 40	>40	20 – 40	≥40
	Summer	20 – 80	70 - >80	20 – 40	40 - >80
	Combined	20 - >100	70 - >100	20 – 70	80 – 90

Table 3.3. Number of individual female black and brown bears exhibiting differences between night (1900-0659) and day (0700-1859) seasonal (spring = late May-Jun; summer = Jul-late Sep; combined = late May-late Sep) habitat use, southcentral Alaska, 1998-2000.

Species	Season	$P < 0.05$	$0.05 \leq P < 0.10$	$P \geq 0.10$	Total
Black	Spring	3	4	20	27
	Summer	4	3	21	28
	Combined	7	7	41	55
Brown	Spring	5	0	12	17
	Summer	10	2	6	18
	Combined	15	2	18	35

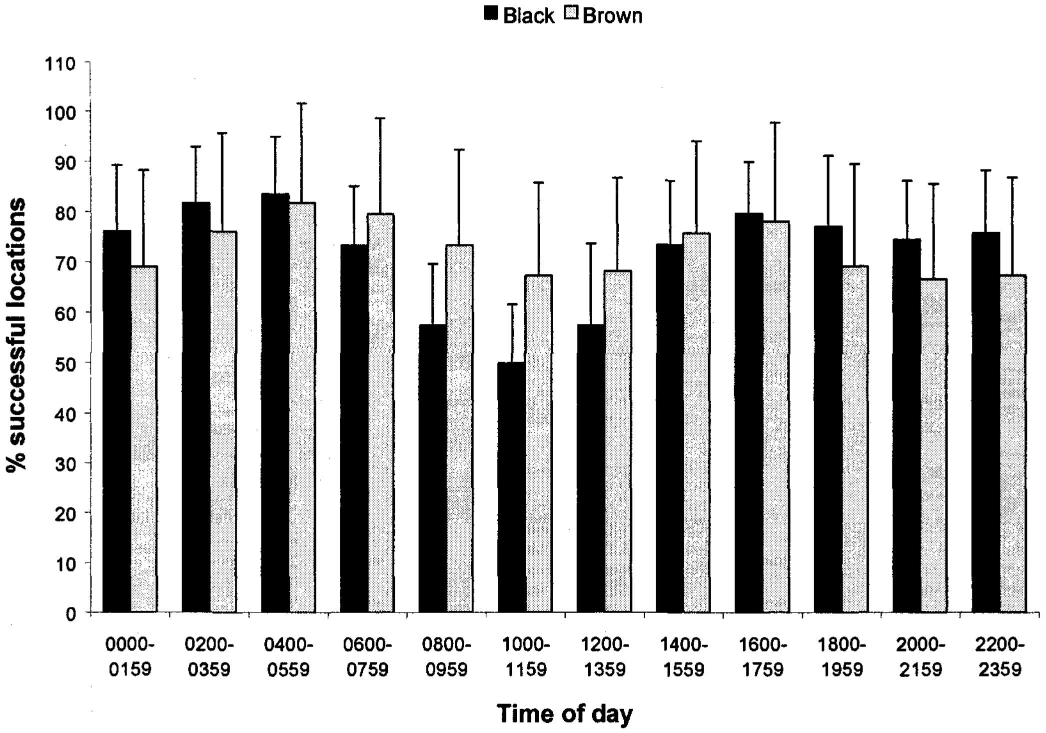

Fig. 3.1. Mean (± SD) percent successful locations by 2-hr interval obtained for female black (*n* = 20) and brown (*n* = 12) bears with GPS collars, southcentral Alaska, May-September, 1998-2000.

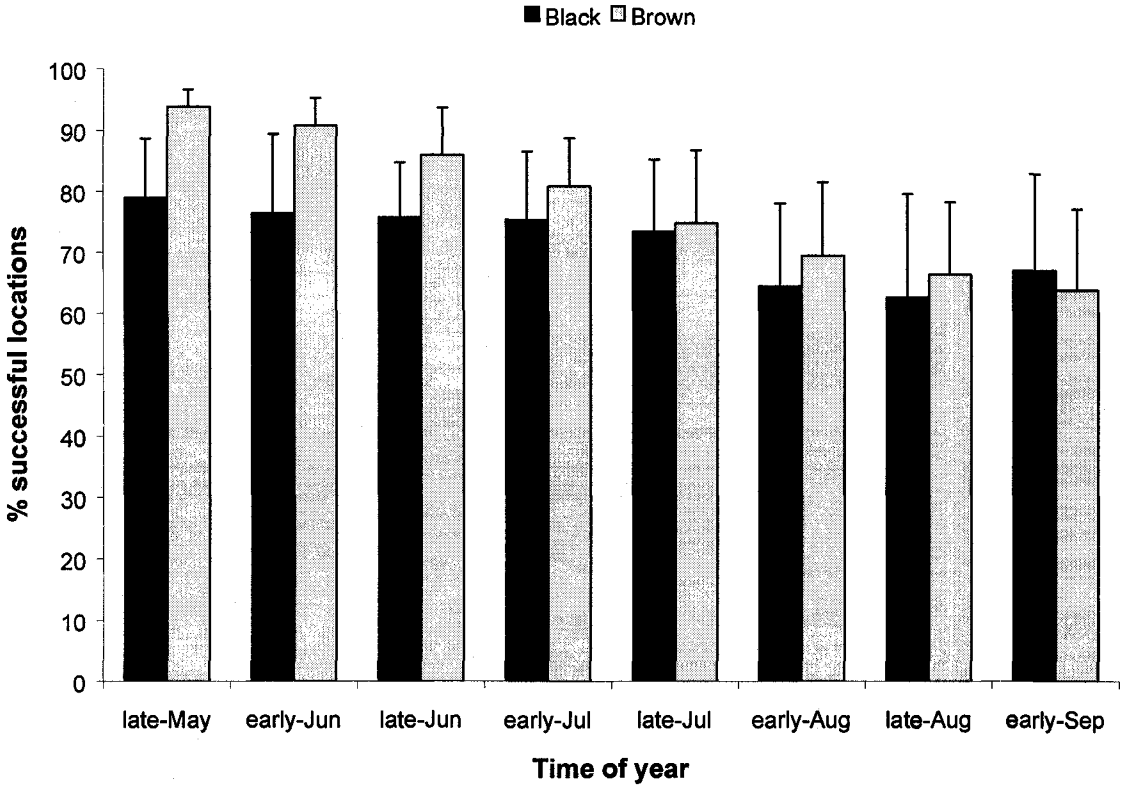

Fig. 3.2. Mean (± SD) percent successful locations by half-month interval obtained for female black ($n = 20$) and brown ($n = 12$) bears with GPS collars, southcentral Alaska, May-September, 1998-2000.

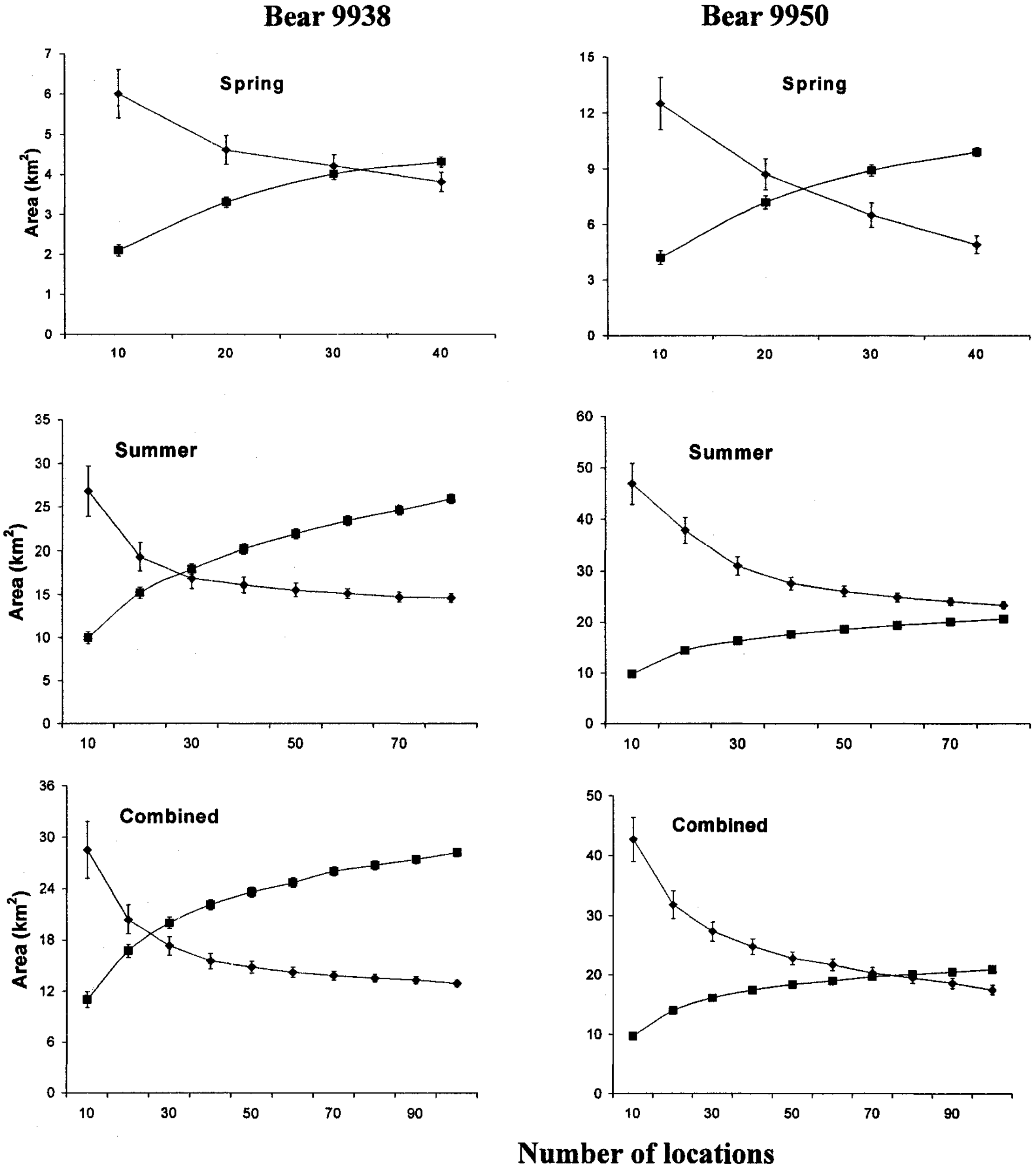

Fig. 3.3. Examples of effects of sample size on area (km^2) estimates (± SE) of spring (late May-Jun), summer (Jul-late Sep), and combined (late May-late Sep) home ranges using minimum convex polygon (squares) and fixed kernel (diamonds) for two female black bears, southcentral Alaska, 2000. Each data point represents 1,000 simulations using randomly-selected subsets of data.

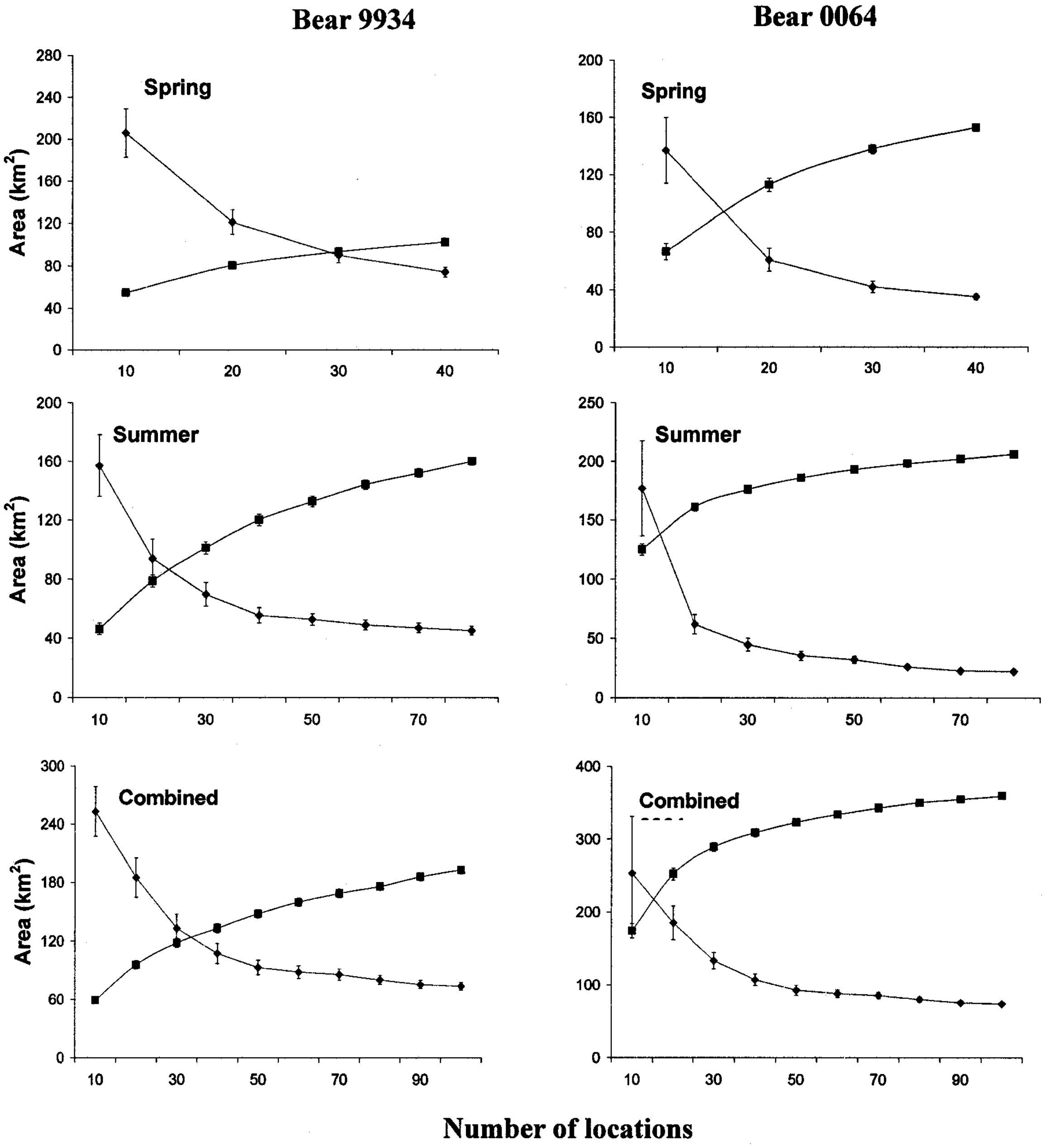

Fig. 3.4. Examples of effects of sample size on area (km^2) estimates (± SE) of spring (late May-Jun), summer (Jul-late Sep), and combined (late May-late Sep) home ranges using minimum convex polygon (squares) and fixed kernel (diamonds) for two female brown bears, southcentral Alaska, 2000. Each data point represents 1,000 simulations using randomly-selected subsets of data.

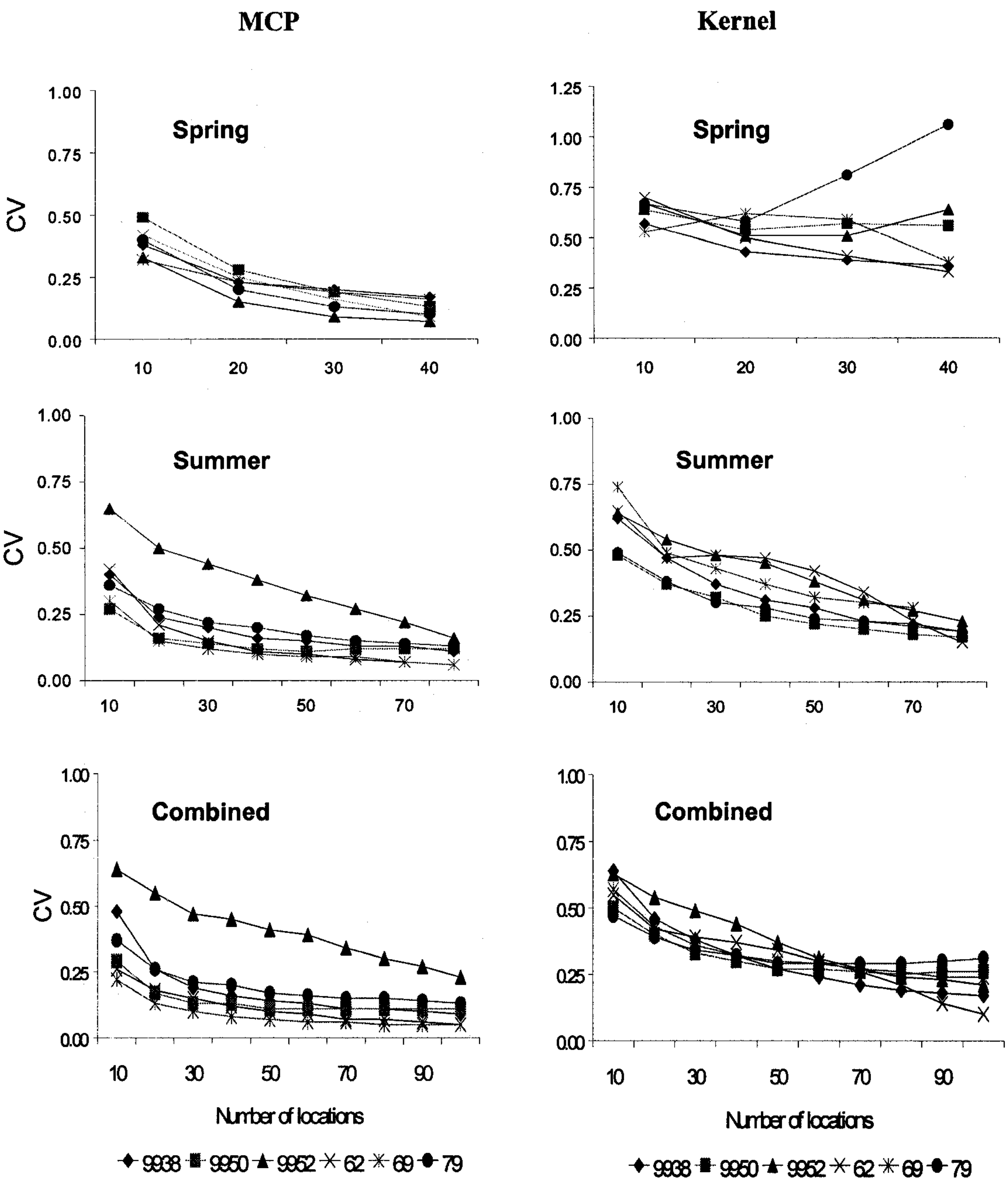

Fig. 3.5. Effect of sample size on coefficient of variation (CV) of home range estimates during spring (late May-Jun), summer (Jul-late Sep), and combined (late May-late Sep), using minimum convex polygon and fixed kernel methods for female black bears, southcentral Alaska, 2000. Each data point represents the mean of 1,000 simulations using randomly-selected subsets of data.

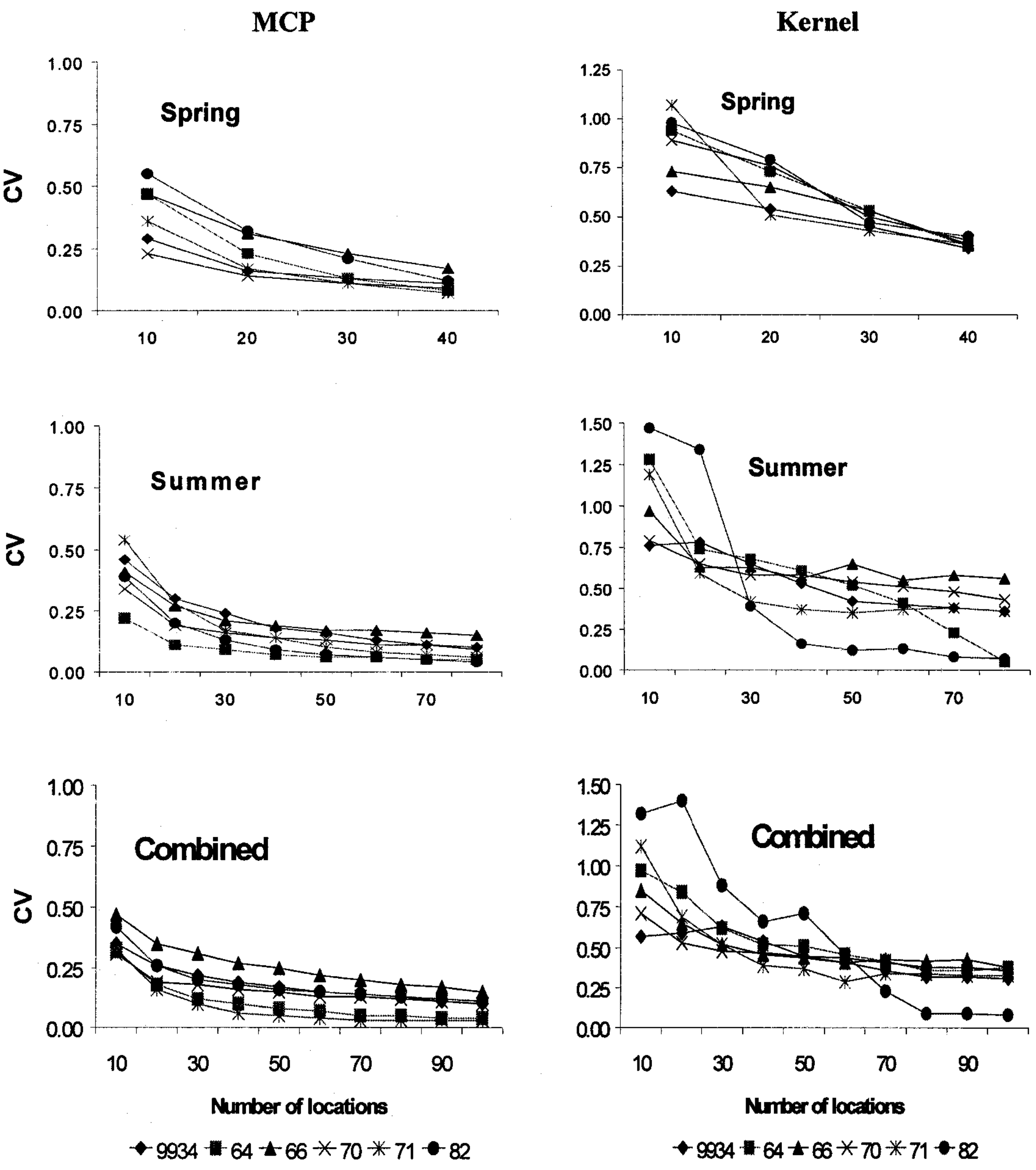

Fig. 3.6. Effect of sample size on coefficient of variation (CV) of home range estimates during spring (late May-Jun), summer (Jul-late Sep), and combined (late May-late Sep), using minimum convex polygon and fixed kernel methods for female brown bears, southcentral Alaska, 2000. Each data point represents the mean of 1,000 simulations using randomly-selected subsets of data.

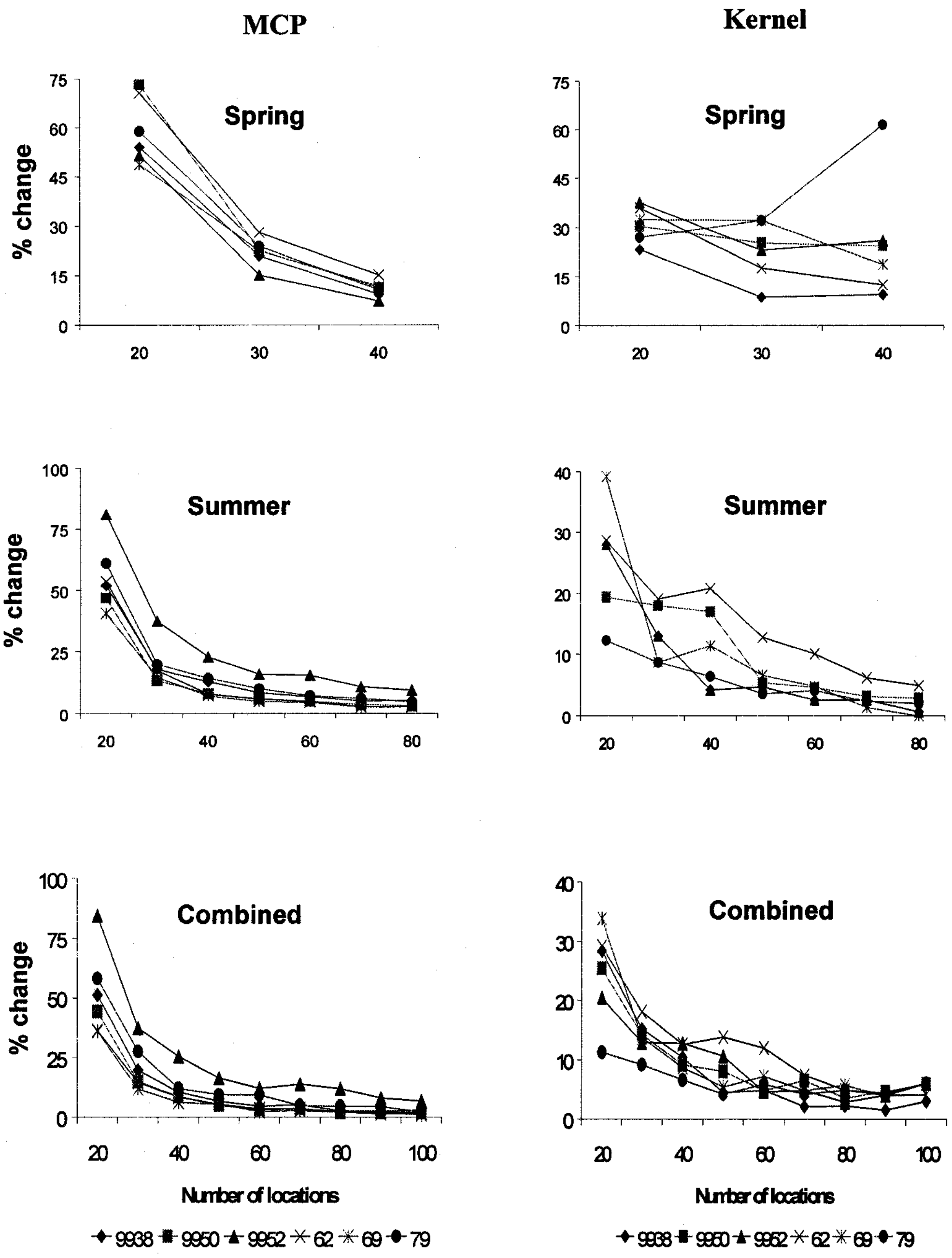

Fig. 3.7. Percent change in female black bear mean home area using successively increasing locations during spring (late May-Jun), summer (Jul-late Sep), and combined (late May-late Sep), southcentral Alaska, 2000. Percent change is relative to mean area estimate for 10 fewer locations. Each data point represents the mean of 1,000 simulations using randomly-selected subsets of data.

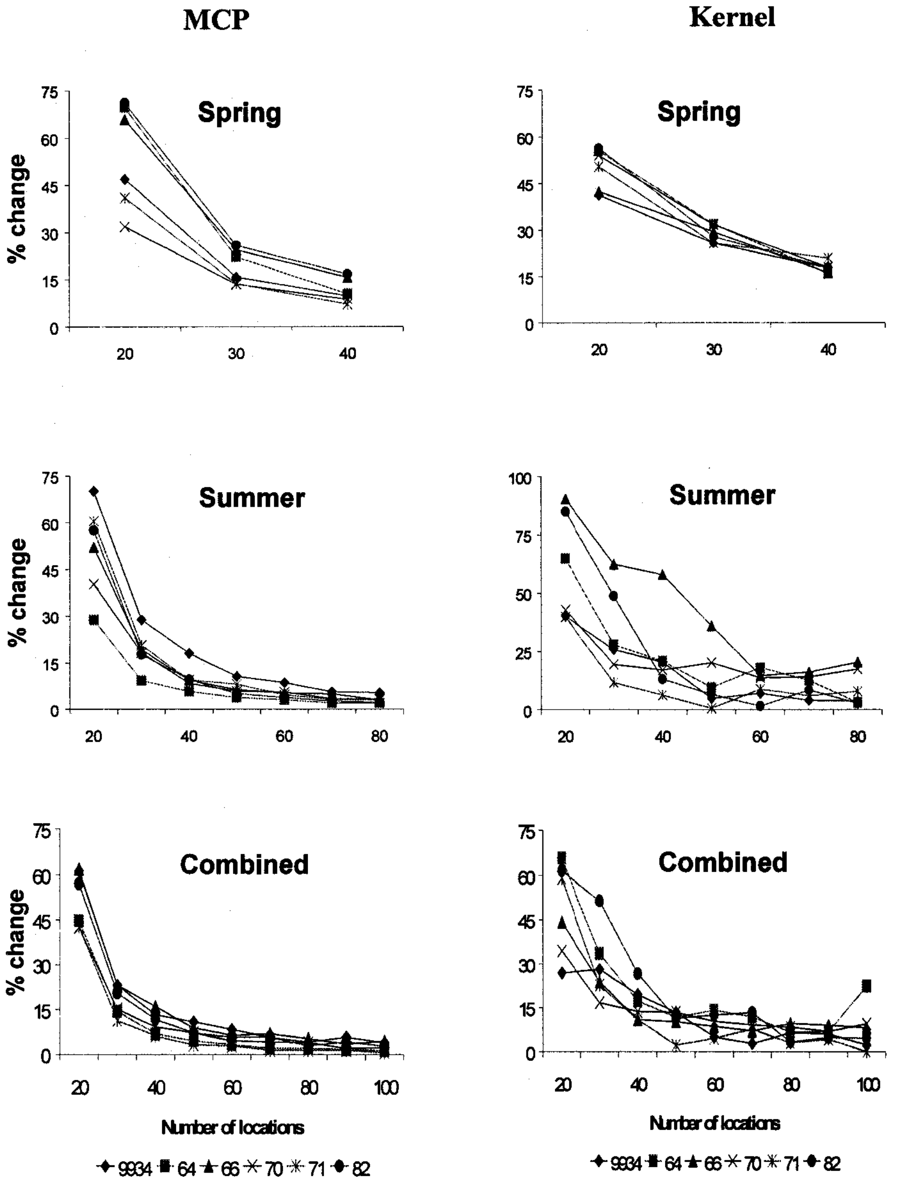

Fig. 3.8. Percent change in female brown bear mean home area using successively increasing locations during spring (late May-Jun), summer (Jul-late Sep), and combined (late May-late Sep), southcentral Alaska, 2000. Percent change is relative to mean area estimate for 10 fewer locations. Each data point represents the mean of 1,000 simulations using randomly-selected subsets of data.

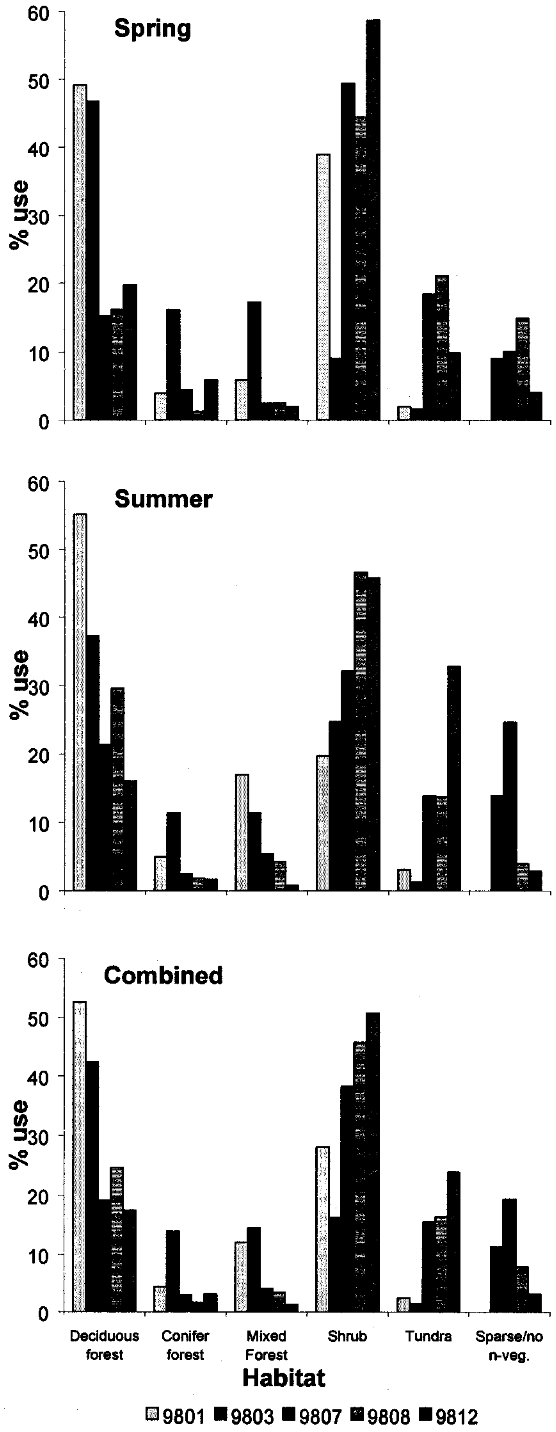

Fig. 3.9. Individual female black bear habitat use during spring (May-Jun), summer (Jul-Sep), and combined, southcentral Alaska, 1998.

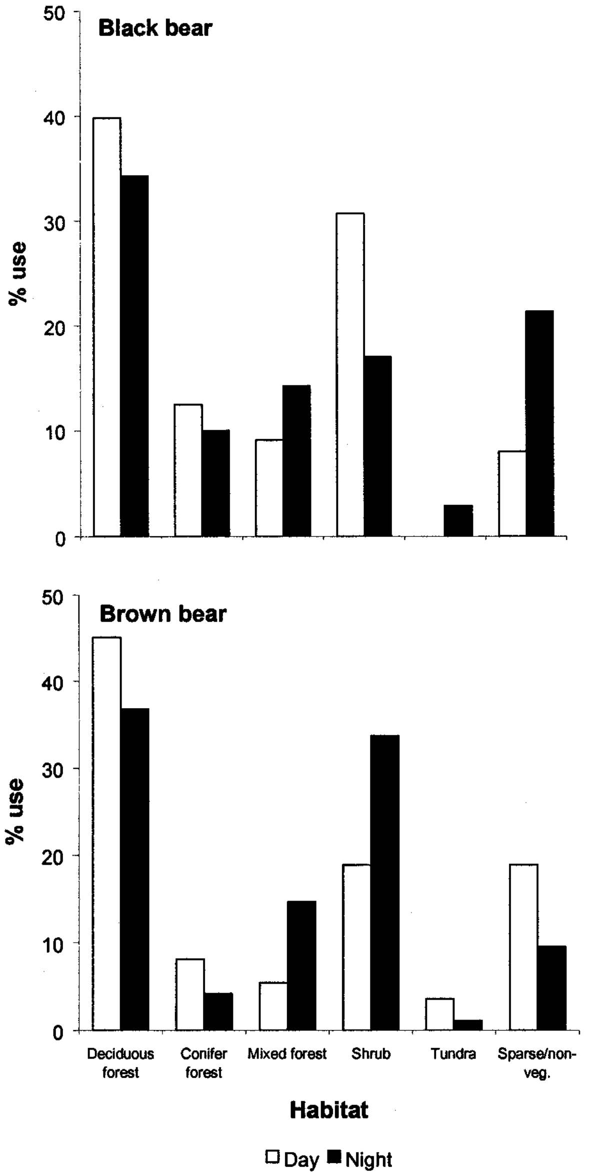

Fig. 3.10. Examples of variation in summer (Jul-Sep) diurnal (0700-1859) and nocturnal (1700-0659) percent habitat use by a female black bear during 1998 and a female brown bear during 2000, southcentral Alaska.

CONCLUSIONS

This study is the first effort to quantify partitioning of food resources by sympatric brown (*Ursus* arctos) and American black (*U. americanus*) bears and relate their assimilated diets to body condition and reproductive performance. Salmon predominated in brown bear assimilated diets in this study area >200 km from the ocean coast, similar findings in brown bear populations (Hilderbrand et al 1999). In contrast, black bears assimilated more vegetation and appeared able to exploit salmon only when salmon abundance was above the long-term mean. When black bears in this study exploited salmon, they assimilated less than one-half the amount of salmon exploited by an allopatric population of black bears (Jacoby et al. 1999). Apparently, presence or interference by 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 assimilated diet, and overall body size of brown bears was comparable to coastal brown bear populations, supporting the importance of salmon to body condition. 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., percent body fat), which was positively associated with salmon assimilated in their diet. Consistently high body condition across years in brown bears was reflected in consistently high reproduction. Brown bears appeared to reduce the realized niche of black bears by altering their use of 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 was associated with lower body condition and reduced reproductive output. I conclude that in this area of Alaska, brown bears formed in part the realized niche of black bears, which resulted in the partitioning of food resources.

Use of GPS collars in this study offered several advantages over other telemetry systems, including collection of data during inclement weather, greater frequency of locations, reduction of human error, and increased cost effectiveness for multi-year studies (Schwartz and Arthur 2001). For home range and habitat studies in remote or large geographic areas, GPS or another satellite-based systems may be the only practical solution.

Because of differences in habitat use I observed, pooling location data for bears within or across seasons is not recommended. As diurnal and nocturnal habitat use also differed, inferences from data collected during only part of the 24-hr period cannot be extrapolated to the entire 24-hour period *a priori*. Management recommendations based on data collected during part of the 24-hour period could be misleading or even detrimental to affected populations. Sampling designs for collecting location data should occur in relation to original study objectives.

I used the above analyses to assess spatial segregation and seasonal habitat selection of sympatric brown and American black bears using population-level inference. My hypothesis of black bear avoidance of brown bears under Fretwell's (1972) ideal despotic distribution model was rejected in part as black bears were positively associated with areas containing brown bear during spring. I surmised this was related to spatially-restricted (i.e., restricted to low elevations) but dispersed availability of food and the spatial resolution used to model resource selection. In contrast, the ideal despotic distribution model was supported by bear resource selection during summer. Black bears were in part displaced by brown bears from the most suitable areas during summer, resulting in black bear use of less suitable areas. That is, black bear access to salmon was restricted by brown bears, causing increased use of vegetation types containing alternate foods. This restriction of use resulted in black bears using areas containing less nutritious forage. Spatial segregation of brown and American black bears apparently occurs when optimal resources are limited or spatially restricted and alternate resources are available to the subordinate species.

Overall, similarities between brown and black bears for preferred and potentially limited food resources will result in spatial co-occupancy only when these resources are dispersed or suitable but less preferred resources are available. I contend that similarities in preferred and potentially limited resources resulted in co-occupancy of areas at moderate to coarse spatial resolutions. I suggest that black bears spatially avoided areas with brown bears which influenced black bears' population-level use of resources, supporting the ideal despotic distribution model. The realized niche of black bears was constrained by brown bears through partitioning of food resources, which varied among years. Reduced access to areas containing salmon caused black bears to forage more extensively in areas containing less predictable or nutritious food sources resulting in lowered body condition and subsequent lowered reproduction. Long-term coexistence of these species in this study area appears dependent on the distribution, abundance, and availability of salmon and berries.

References

Fretwell SD (1972) Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey

Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C (1999) The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Can J Zool 77:132-138

Jacoby ME, Hilderbrand GV, Servheen C, Schwartz CC, Arthur SM, Hanley TA, Robbins CT, Michener R (1999) Trophic relations of brown and black bears in several North American ecosystems. J Wildl Manage 63:921-929

Schwartz CC, Arthur SM (1999) Radio-tracking large wilderness mammals: integration of GPS and ARGOS technology. Ursus 11:261-273

Appendix

Negative binomial generalized linear mixed models with fixed effects were developed using all model terms in factorial combination described in Chapter 2. Suites of models including global (all model terms) and null (intercept only) models were developed for brown and American black bears in southcentral Alaska during spring (May-June) and summer (July-September) 2000 using the 2 km^2 and 4 km^2 grids. Model output (Table A.1) is for descriptive purposes only; the intent is to provide insight to individuals considering black or brown bear resource selection studies.

Table A.1 Model-fitting results for resource selection of 2 km^2 and 4 km^2 cells by brown and American black bears in southcentral Alaska during spring (May-June) and summer (July-September) 2000. Models are compared according to number of parameters (*K*), Akaike's Information Criterion corrected for small sample size (AIC$_c$), the difference in AIC$_c$ from best-fitting model (ΔAIC$_c$), and relative rank by species and season.

				2 km^2			4 km^2		
Species	Season	Model[a]	*K*	AIC$_c$	ΔAIC$_c$	Rank	AIC$_c$	ΔAIC$_c$	Rank
Brown	Spring	ELEV, ELEV^2	4	5836.2	0.0	1	2564.3	0.0	1
		ELEV, ELEV^2, BLBEAR	5	5837.6	1.4	2	2564.5	0.2	2
		DISSTREAM, ELEV, ELEV^2	5	5838.0	1.8	3	2566.2	1.9	3
		DISSTREAM, ELEV, ELEV^2, BLBEAR	6	5839.4	3.2	4	2566.4	2.1	4
		VEG, ELEV, ELEV^2	9	5840.6	4.4	5	2571.6	7.3	5
		VEG, ELEV, ELEV^2, BLBEAR	10	5841.7	5.5	6	2571.8	7.5	6
		VEG, DISSTREAM, ELEV, ELEV^2	10	5842.3	6.1	7	2573.6	9.3	8
		VEG, DISSTREAM, ELEV, ELEV^2, BLBEAR	11	5843.2	7.0	8	2573.8	9.5	9

Table A.1 (Continued)

Species	Season	Model[a]
Brown	Spring	VEG, DISSTREAM
		VEG, DISSTREAM, BLBEAR
		VEG
		VEG, BLBEAR
		DISSTREAM
		DISSTREAM, BLBEAR
		NULL
		BLBEAR
Brown	Summer	VEG, DISSTREAM, ELEV, $ELEV^2$
		VEG, DISSTREAM, ELEV, $ELEV^2$, BLBEAR
		DISSTREAM, ELEV, $ELEV^2$

	2 km^2			4 km^2		
K	AIC$_c$	ΔAIC$_c$	Rank	AIC$_c$	ΔAIC$_c$	Rank
8	5853.9	17.7	9	2575.1	10.8	11
9	5855.4	19.2	10	2576.2	11.9	14
7	5860.2	24.0	11	2575.4	11.1	13
8	5861.6	25.4	12	2576.4	12.1	15
3	5863.0	26.8	13	2573.5	9.2	7
4	5865.0	30.0	14	2575.3	11.0	12
2	5865.0	28.8	15	2574.6	10.3	10
3	5866.9	30.7	16	2576.2	12.1	15
10	11846.0	0.0	1	5071.6	4.1	3
11	11847.9	1.9	2	5073.2	5.7	4
5	11849.3	3.3	3	5067.5	0.0	1

Table A.1 (Continued)

Species	Season	Model[a]
Brown	Summer	DISSTREAM, ELEV, ELEV^2, BLBEAR
		VEG, DISSTREAM
		VEG, DISSTREAM, BLBEAR
		DISSTREAM
		DISSTREAM, BLBEAR
		VEG, ELEV, ELEV^2, BLBEAR
		VEG, ELEV, ELEV^2
		ELEV, ELEV^2, BLBEAR
		ELEV, ELEV^2
		NULL
		BLBEAR
		VEG

	2 km^2			4 km^2		
K	AIC$_c$	ΔAIC$_c$	Rank	AIC$_c$	ΔAIC$_c$	Rank
6	11850.5	4.5	4	5069.2	1.7	2
8	11867.4	21.4	5	5074.5	7.0	5
9	11869.3	23.3	6	5076.2	8.7	6
3	11872.1	26.1	7	5076.7	9.2	7
4	11873.4	27.4	8	5078.1	10.6	8
10	11918.9	72.9	9	5105.7	38.2	9
9	11919.2	73.2	10	5076.7	9.2	7
5	11925.3	79.3	11	5107.8	40.3	13
4	11926.8	80.8	12	5106.4	38.9	11
2	11987.5	141.5	13	5125.8	58.3	14
3	11987.6	141.6	14	5127.5	60.0	15
7	11989.8	143.8	15	5105.8	38.3	10

Table A.1 (Continued)

Species	Season	Model[a]
Brown	Summer	VEG, BLBEAR
Black	Spring	VEG, ELEV, ELEV^2
		VEG, ELEV, ELEV^2, BRBEAR
		VEG, DISSTREAM, ELEV, ELEV^2
		VEG, DISSTREAM, ELEV, ELEV^2, BRBEAR
		VEG, DISSTREAM
		VEG, DISSTREAM, BRBEAR
		VEG
		DISSTREAM, ELEV, ELEV^2
		VEG, BRBEAR
		DISSTREAM, ELEV, ELEV^2, BRBEAR

	2 km^2			4 km^2		
K	AIC$_c$	ΔAIC$_c$	Rank	AIC$_c$	ΔAIC$_c$	Rank
8	11990.0	144.0	16	5107.2	39.7	12
9	3029.2	0.0	1	1267.8	6.0	6
10	3031.0	1.8	2	1269.7	7.9	9
10	3031.2	2.0	3	1273.7	11.9	13
11	3033.6	4.4	4	1274.2	12.4	14
8	3043.4	14.2	5	1271.4	9.6	11
9	3045.4	16.2	6	1268.5	6.7	7
7	3050.3	21.1	7	1270.7	8.9	10
5	3050.3	21.1	7	1261.8	0.0	1
8	3052.3	23.1	8	1264.3	2.5	3
6	3052.4	23.2	9	1272.6	10.8	12

Table A.1 (Continued)

Species	Season	Model[a]
Black	Spring	ELEV, ELEV^2
		ELEV, ELEV^2, BRBEAR
		DISSTREAM
		DISSTREAM, BRBEAR
		NULL
		BRBEAR
Black	Summer	VEG, ELEV, ELEV^2
		VEG, ELEV, ELEV^2, BRBEAR
		VEG, DISSTREAM, ELEV, ELEV^2
		VEG, DISSTREAM, ELEV, ELEV^2, BRBEAR
		VEG, DISSTREAM

	2 km^2			4 km^2		
K	AIC$_c$	ΔAIC$_c$	Rank	AIC$_c$	ΔAIC$_c$	Rank
4	3055.1	25.9	10	1263.0	1.2	2
5	3057.1	27.9	11	1264.9	3.1	4
3	3061.7	32.5	12	1268.8	7.0	8
4	3063.9	34.7	13	1266.9	5.1	5
2	3094.8	65.6	14	1274.7	12.9	15
3	3096.4	67.2	15	1276.4	14.6	16
9	6607.9	0.0	1	2909.2	3.0	8
10	6608.2	0.3	2	2910.7	4.5	12
10	6608.8	0.9	3	2909.0	2.8	8
11	6609.2	1.3	4	2910.3	4.1	11
8	6614.8	6.9	5	2906.2	0.0	1

Table A.1 (Continued)

					$2\ km^2$			$4\ km^2$	
Species	Season	Model[a]	*K*	AIC_c	ΔAIC_c	Rank	AIC_c	ΔAIC_c	Rank
Black	Summer	VEG, DISSTREAM, BRBEAR	9	6614.9	7.0	6	2907.5	1.3	4
		ELEV, $ELEV^2$	4	6619.1	11.2	7	2906.3	0.1	2
		DISSTREAM, ELEV, $ELEV^2$	5	6619.1	11.2	7	2907.4	1.2	3
		DISSTREAM, ELEV, $ELEV^2$, BRBEAR	6	6619.4	11.5	8	2908.8	2.6	7
		ELEV, $ELEV^2$, BRBEAR	5	6619.5	11.6	9	2907.8	1.6	5
		VEG	7	6622.8	14.9	10	2912.0	5.8	13
		VEG, BRBEAR	8	6622.8	14.9	11	2913.4	7.2	14
		DISSTREAM	3	6632.2	24.3	12	2908.1	1.9	6
		DISSTREAM, BRBEAR	4	6633.1	25.2	13	2909.6	3.4	10
		NULL	2	6651.4	43.5	14	2918.0	11.8	15
		BRBEAR	3	6652.4	44.5	15	2919.8	13.6	16

Table A.1 (Continued)

[a] Model terms include (ELEV), quadratic elevation ($ELEV^2$), distance to nearest stream containing salmon (DISSTREAM), dominant vegetation type (VEG), intensity of black bear use (BLBEAR), intensity of brown bear use (BRBEAR), and intercept only (NULL).