

# Home range and movements of female brown bears in southwestern Alaska

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**Abstract:** Between 1993 and 2003, 40 adult female brown bears (*Ursus arctos*) were radiocollared and monitored in the southwest Kuskokwim Mountains of Alaska. The 95% kernel home range size for individuals with  $\geq 50$  relocations ( $n = 20$ ) ranged from 93–623 km<sup>2</sup> ( $\bar{x} = 356$  km<sup>2</sup>). Bears occupied lower elevations during July and August ( $\bar{x} = 454$  m) when salmon (*Oncorhynchus* spp.) were available and higher elevations in September ( $\bar{x} = 520$  m), presumably to feed on berries, ground squirrels (*Spermophilus parryii*), and caribou (*Rangifer tarandus*). During the denning period, bears moved to higher average elevations ( $\bar{x} = 632$  m), generally remaining through June ( $\bar{x} = 570$  m). Radiomarked females entered the den in mid October and exited in mid May. There was fidelity to denning areas, with an average distance between consecutive dens of 4.5 km (SD = 3.1). Females with cubs were found at higher average elevations than females without young or with yearlings. Radiomarked females were found closer to anadromous streams from 16 July–15 August, coinciding with chinook (*O. tshawytscha*), chum (*O. keta*), and sockeye salmon (*O. nerka*) availability. Beginning in 1998, chinook and chum salmon escapement was low in the Kuskokwim drainage. There was an inverse relationship between measures of salmon availability and bear distances to anadromous streams. This indicates that although the study area was at the fringe of salmon range, salmon abundance influenced bear seasonal movements and distribution. With reduced salmon availability, this area may support a lower bear density, and brown bear population management should be considered in salmon escapement goals.

**Key words:** anadromous, denning, elevation, kernel, *Oncorhynchus*, radio telemetry, salmon, *Ursus arctos*

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Brown bears (*Ursus arctos*) have historically been an important source of food and hides for Native residents of southwest Alaska (Van Daele et al. 2001). In 1991 and 1992, state and federal regulatory boards liberalized brown bear hunting regulations for subsistence users in southwest Alaska. The bear population affected by this liberalization had never been investigated, and little was known about its size, distribution, or behavioral characteristics.

Home range estimates can indicate the ecological requirements of animals because home ranges include all resources used by a resident (Seaman and Powell

1990). Home ranges and the movements within them are behavioral manifestations of basic biological requirements, such as food, shelter, and mates. Brown bear home range size is a function of habitat quality and population density (Nagy and Haroldson 1990). Several studies documented habitat use and movement patterns of coastal (Berns et al. 1980, Glenn and Miller 1980, Schoen et al. 1986, Hamilton and Bunnell 1987, Barnes 1990, Ballard et al. 1993) and interior (Ballard et al. 1982) brown bears. These studies demonstrated how use of salmon (*Oncorhynchus* spp.) streams varied among bear populations. Brown bears in British Columbia ranged widely during the berry season, then restricted movement while feeding on salmon (Hamilton and Bunnell 1987). On the Alaska Peninsula (Glenn and Miller 1980), bears moved greater distances in spring than in summer and fall. Schoen et al. (1986) demonstrated that a portion of the Admiralty Island population did not feed on salmon, instead foraging in interior alpine and subalpine habitats.

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From June 1993 to June 2003, a study was conducted to: (1) estimate the density of brown bears in the southwestern Kuskokwim Mountains; (2) delineate home ranges, seasonal use areas, and movements; (3) estimate sex and age structure, productivity, and survival rates; and (4) estimate harvest. Van Daele et al. (2001) presented perspectives of bear conservation in southwest Alaska, described the interaction between biologists and indigenous peoples, and reported biological results from the first 5 years of this study (1993–97). Here, we present the 10-year culmination (1993–2003) of home range and movement data (objective 2) of radiomarked female brown bears in the Kuskokwim Mountains of southwest Alaska.

### Study area

The study area was in the southwest Kuskokwim Mountains (approximately 60°N, 159°W), midway between Dillingham and Bethel, Alaska. It encompassed approximately 9,600 km<sup>2</sup> of public lands administered by Yukon Delta National Wildlife Refuge (48%), Togiak National Wildlife Refuge (19%), State of Alaska (29%), Wood-Tikchik State Park (3%), and Bureau of Land Management (1%). There were no roads, private inholdings, or permanent structures within the study area. Recent use was limited to hunters, anglers, and other recreational users.

Van Daele et al. (2001) described the study area. Elevations ranged from 75 m in the western portion of the study area (tundra plains) to 1,534 m (glacial peaks). The steep glacial peaks constituted the hydrographic divide between the Nushagak River to the east, the Togiak River to the south, and the Kuskokwim watershed to the west and north. Mean annual precipitation was 89 cm, including 178 cm of snow. Snow persisted in lower elevations from late October to May; vegetation developed rapidly during the short growing season. Mean maximum and minimum temperatures were –10.5°C and –16.5°C in January and 18.5°C and 7°C in July, respectively (National Weather Service, Bethel, Alaska, USA, unpublished data). Mountainous portions of the area (>600 m) were sparsely vegetated with low-growing shrubs and herbaceous plants. Mid-elevation areas (300–600 m) were covered with dwarf shrubs, including Labrador tea (*Ledum palustre*), crowberry (*Empetrum nigrum*), and sedges (*Carex* spp.) interspersed with dense stands of willow (*Salix* spp.) and alder (*Alnus* spp.). Lowland areas (75–300 m) were dominated by bog willow (*S. arctica*), dwarf birch (*Betula nana*), and various berry-producing shrubs

including lowbush blueberry (*Vaccinium uliginosum*), cranberries (*V. microcarpus* and *V. vitis-idaea*), and bearberry (*Arctostaphylos alpina*). Cottonwoods (*Populus balsamifera*) dominated the overstory in riparian areas.

The Kilbuck caribou (*Rangifer tarandus*) herd (~5,000 animals) resided in the study area, and in recent years the area was used seasonally by a portion of the Mulchatna caribou herd (~20,000 animals). Moose (*Alces alces*) occurred at low densities along riparian corridors. Area streams provided spawning and rearing habitat for chinook (*O. tshawytscha*), sockeye (*O. nerka*), chum (*O. keta*), and coho salmon (*O. kisutch*). Rainbow trout (*O. mykiss*), lake trout (*Salvelinus namaycush*), arctic grayling (*Thymallus arcticus*), and Dolly Varden (*S. malma*) were resident (Marrow 1980).

### Methods

Capture operations were conducted in 1993, 1994, 1997, 2000, and in 2003 (collar removal only). Capture methodology is detailed in Van Daele et al. (2001). We located bears using fixed wing aircraft (PA-18 Super-Cub) and captured bears by darting them from a Hughes 500D helicopter using a powder fired Cap-Chur rifle (Palmer Cap-Chur Inc., Powersprings, Georgia, USA). Bears were chemically immobilized using Telazol® (A.H. Robbins Company, Richmond, Virginia, USA; Taylor et al. 1989). We marked each bear with individually numbered ear tags and lip tattoos. Selected bears were fitted with radiotelemetry collars (Telonics Inc., Mesa, Arizona, USA). We weighed bears by suspending them below the helicopter in a cargo net attached to a dial scale. Specific capture summaries are provided in earlier reports (Miller et al. 1995; Kovach 1997, 2001, 2003).

We collected standard measurements, hair and blood samples, and a first premolar from each captured bear (Van Daele et al. 2001). Cementum-aging analysis was provided by Matson's Laboratory (Milltown, Montana, USA; Matson et al. 1993).

We conducted radiotelemetry flights monthly while bears were denned (generally Nov–Mar) and weekly to biweekly while bears were active. Fixed-wing aircraft (PA-18 SuperCub, Cessna 185, Cessna 206, or Maule M-7) equipped with 2 wing-strut mounted 2-element H antennas were used for telemetry flights. We used a global positioning system (GPS) to delineate bear locations and standardized forms to record data on habitat, bear activities, and group composition (Van Daele et al. 2001). Ages of offspring for radiomarked females were determined from known birth years

(observed at first den emergence;  $n = 161$ ) or visually estimated ( $n = 16$ ). Offspring were grouped into 3 categories for analysis: cubs (<1 year old), yearlings (1 year old), and older offspring (>1 year old). Den locations of radiomarked bears were estimated during radiotelemetry flights in the winter. We revisited den sites by air in spring once the den was opened to refine the location. We estimated our aerial radiotelemetry error using ArcInfo (version 8.1, Environmental Systems Research Institute, Redlands, California, USA) to calculate straight line distances between coordinates collected from ground investigations of mortalities and dropped collars (known location) and coordinates collected during previous telemetry flights of those same locations (estimated location).

Grizzly bear home ranges vary in size throughout North America (Nagy and Haroldson 1990); however, it is difficult to compare previous estimates because methods used to collect data and calculate areas varied among studies (Interagency Grizzly Bear Committee 1987). Of the nonparametric methods for estimating animal home ranges, the fixed kernel has been recently considered the method of choice (Worton 1995; Seaman et al. 1998, 1999; Powell 2000; Belant and Follmann 2002). Harris et al. (1990) suggested using at least 2 home range estimators with any dataset, one of which being the minimum convex polygon (MCP) for comparison with other studies. Kernohan et al. (2001) suggested this was an inadequate justification because comparisons are generally unreliable due to its sensitivity to sample size and outliers. However, recognizing these limitations, we report MCP calculations for comparative purposes.

Home range and movement analyses were limited to relocations >6 days apart to exclude capture and census operations; duplicated den locations were also excluded. Home range analyses were limited to individuals with  $\geq 50$  total relocations (Seaman et al. 1999; E.O. Garton, University of Idaho, Moscow, Idaho, USA, personal communication, 2002), although even with samples of >50 locations, variability of brown bear home range estimates can be high (Arthur and Schwartz 1999, Belant and Follmann 2002). Minimum convex polygon (100%) home ranges, fixed kernel (95%) home ranges, and distances between relocations and successive dens were calculated using the animal movement extension (Hooge et al. 1999) for ArcView (version 3, Environmental Systems Research Institute, Redlands, California, USA). Least squares cross validation (LSCV) was used to calculate the smoothing parameter or kernel bandwidth ( $h_{LSCV}$ ; Kernohan et al. 2001) for the fixed kernel

home range estimates (Hooge et al. 1999, Seaman et al. 1999, Powell 2000). The smoothing parameter controls the amount of variation in each component of the estimate, defining the bandwidth of the kernel. Least-squares cross validation resembles a jackknife estimator, using subsets of data to determine the bandwidth that yields the lowest measure of estimated error (Blundell et al. 2001).

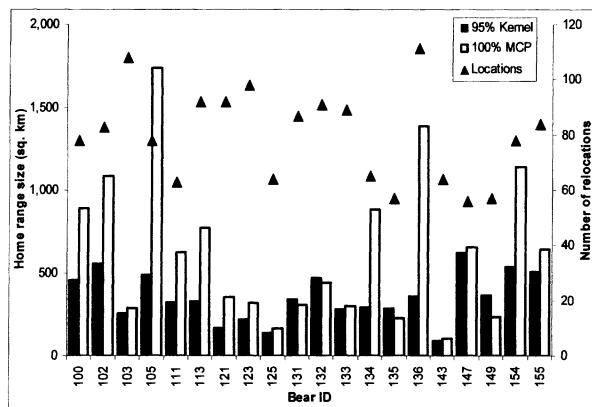
No objective method exists at present to tie bandwidth to biology or to location error (Powell 2000). After visual inspection of our data, we believed the  $h_{LSCV}$  caused the home range to be overestimated for one individual (Bear 152; see Results). Therefore, we also performed a separate analysis with an *a priori* selected  $h$ -value ("plug-in",  $h_{pi}$ ; Kernohan et al. 2001), that being the maximum value from the other 20 study individuals.

We compared elevational use of our radiomarked bears by year, season, and reproductive status. Elevation was calculated from a digital elevation model (US Geological Survey, Alaska Geospatial Data Clearinghouse, Anchorage, Alaska, USA) with 30-m grid cells using the spatial analyst extension (Environmental Systems Research Institute, Redlands, California, USA) for ArcView.

Suspecting an influence on bear movements by the availability of salmon, we evaluated the distances from anadromous fish streams from radiomarked bears relocations. The 2002 Draft Anadromous Water Catalog (Alaska Department of Fish and Game 2002) was used for salmon stream distance analyses. The non-denning period (Jun–Sep) was divided into half-month increments for analysis. Distance to the nearest anadromous stream for each bear relocation was measured. No direct measure of salmon run sizes were made for the Kuskokwim River drainage (D. Molyneaux, Alaska Department of Fish and Game, Commercial Fish Department, Anchorage, Alaska, USA, personal communication, 2004).

To gauge relative size of salmon runs, we developed an index from available weir escapement data for chinook, chum, and coho within the Kuskokwim River drainage (D. Molyneaux, personal communication, 2004). The annual index for each weir by species was calculated by dividing the number of salmon recorded at the weir in a single year by the median value for all years that the weir was operational (range = 4–11 years). The annual index was the median of the individual weir median values for each species.

We tested for differences in elevational use and distances to salmon streams using the Mann-Whitney  $U$ -test and Kruskal-Wallis  $k$ -test (Steel et al. 1997). Linear



**Fig. 1.** Kernel (95%) and minimum convex polygon (100% MCP) home ranges, and number of relocations of radiomarked female brown bears, Kuskokwim Mountains, southwest Alaska, 1993–2003.

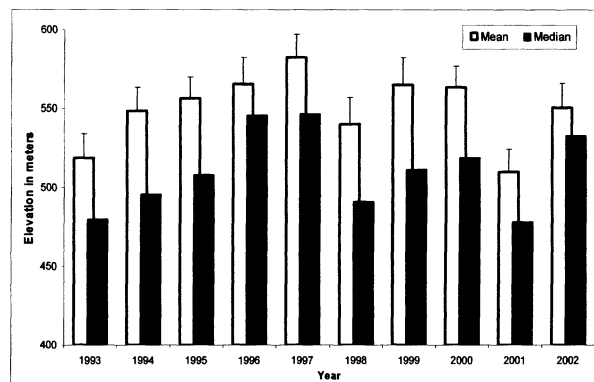
regression was used to identify the relationship between days between relocations and successive distances, and salmon escapement indices and average distances to the nearest anadromous stream. All tests were performed with SYSTAT (version 9.0, SPSS, Inc., Chicago, Illinois, USA); we assumed statistical significance at  $P < 0.05$ .

## Results

### Captures and monitoring

During 5 capture efforts, we captured 52 individual female brown bears, 40 of which received radiotransmitters. Radiocollars were deployed in 1993 ( $n = 22$ ), 1994 ( $n = 8$ ), and 2000 ( $n = 10$ ). We were limited to replacing collars in 1997 ( $n = 25$ ; Van Daele et al. 2001) and removing collars in 2003 ( $n = 19$ ). Ages of captured female bears ranged from 0.5 to 29.5 years. Weights of adult ( $>5.5$  years) females averaged 133 kg ( $SD = 22$ ).

From June 1993 to June 2003, we averaged 20 days between relocations for individual bears during the non-denning period (Jun–Sep;  $SD = 10.4$ , range = 7–100), excluding captures and census efforts. Approximately 67% of relocations for bears away from their dens were determined by visual confirmation; the telemetry error in those cases was zero. For bears relocated in dense vegetation with no visual confirmation (approximately 33%) or for bears in the den, our estimated mean radiotelemetry error was 292 m ( $SD = 212$  m,  $n = 37$ ). During this study, we collected 3,840 relocations from radiomarked females; 725 of these relocations were of females accompanied by young ( $n = 265$  with cubs,  $n = 460$  with yearlings or older offspring). For females



**Fig. 2.** Mean ( $\pm SE$ ) and median elevation occupied annually by radiomarked female brown bears, Kuskokwim Mountains, southwest Alaska, 1993–2002.

initially radiomarked in 1993 or 1994 and followed for  $>3$  years ( $n = 27$ ), we collected an average of 80 unique relocations (range = 29–128).

### Home ranges

Sample sizes were too small (range = 3–14 locations) to estimate home range sizes for individual bears by year, therefore years were combined. Home ranges of bears ( $n = 20$ ) with  $\geq 50$  total relocations ( $\bar{x} = 79.7$  relocations) varied considerably for MCP (range = 104–1,736  $km^2$ ) and 95% kernel (range = 93–623  $km^2$ ) estimators (Fig. 1). Mean MCP sizes averaged 628  $km^2$  ( $SD = 445$ , median = 532  $km^2$ ) and kernel sizes averaged 357  $km^2$  ( $SD = 146$ , median = 338  $km^2$ ).

Bear 152 was excluded from home range and movement analyses because she occupied a substantially larger home range (MCP = 2,935  $km^2$ ; 95% kernel  $h_{lscv} = 5,208$   $km^2$ ;  $n = 75$  relocations). The calculated  $h_{lscv}$  for Bear 152 was 9.49, substantially greater than those for other bears ( $h_{lscv}$  range = 0.9–3.61). The home range calculated using  $h_{pi}$  ( $h_{pi} = 3.61$ ) produced a 95% kernel home range estimate of 2,387  $km^2$ .

### Elevational use

Mean elevational use varied by month ( $k = 238.042$ ,  $P < 0.001$ ). Radiomarked bears occupied lower elevations during July and August ( $\bar{x} = 454$  m,  $SD = 197$ ) and moved to higher elevations in September ( $\bar{x} = 520$  m,  $SD = 197$ ). Bears moved to higher average elevations during denning (Oct–May;  $\bar{x} = 632$  m,  $SD = 240$ ), and remained through June ( $\bar{x} = 570$  m,  $SD = 221$ ). Elevational use also differed annually between 1993 and 2002 ( $k = 17.848$ ,  $P = 0.037$ ; Fig. 2). Reproductive status was a factor in non-denning elevational use; females with cubs were found at higher average

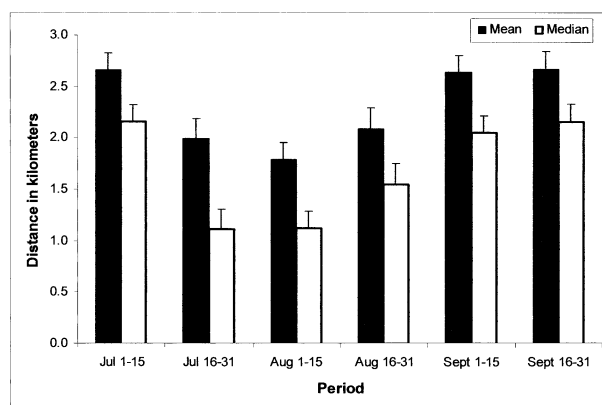


Fig. 3. Mean ( $\pm$ SE) and median distance radiomarked female brown bears were to nearest anadromous stream by period, Kuskokwim Mountains, southwest Alaska, 1993–2002.

elevations ( $\bar{x}$  = 549 m) than solitary females or females with yearlings ( $\bar{x}$  = 508 m,  $U$  = 63082.5,  $P$  = 0.003;  $\bar{x}$  = 493 m,  $U$  = 35645.0,  $P$  = 0.001; respectively).

#### Effects of salmon availability

Chinook salmon were present in the study area by mid-July, followed closely by chum and sockeye salmon. Coho salmon arrived in the study area in late August and early September (M. Rearden, US Fish and Wildlife Service, Bethel, Alaska, USA, personal communication, 1997). There were no foraging sites in the study area where large numbers of bears congregated. We found that distances to salmon streams during 16–31 July and 1–15 August were similar ( $U$  = 12710,  $P$  = 0.848) as were the 1–15 July, 16–31 August, 1–15 September, and 16–30 September periods ( $k$  = 6.258,  $P$  = 0.100; Fig. 3); however, marked bears were found closer to streams during 16 July–15 August ( $U$  = 63239.5,  $P$  = 0.000) than other periods. Reproductive status of females did not influence the distance of relocations from anadromous streams during 16 July–15 August ( $k$  = 2.774,  $P$  = 0.596).

During 16 July–15 August, bears were found on average closer to anadromous streams in 1996 ( $\bar{x}$  = 1.2 km<sup>2</sup>, SD = 1.1) and farthest in 2002 ( $\bar{x}$  = 2.3 km<sup>2</sup>, SD = 6.7); however, the differences were not significant ( $k$  = 15.797,  $P$  = 0.071). We found an inverse relationship between salmon escapement indices and bear distances to anadromous streams between 1993 and 2002 ( $r^2$  = 0.558,  $P$  = 0.013); bears maintained greater average distances from anadromous streams when salmon escapement was low (Fig. 4).

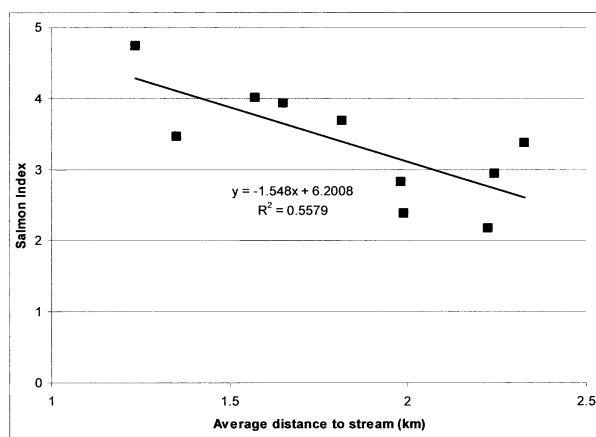


Fig. 4. Relationship between salmon escapement indices and female brown bear distances to anadromous streams, 16 Jul–15 Aug, Kuskokwim Mountains, southwest Alaska, 1993–2002.

#### Dens

On average, radiomarked females in southwest Alaska entered their den in mid October and exited in mid May. Overall, radiomarked bears displayed fidelity to denning areas; the grand mean distance between consecutive dens was 4.5 km (range = 0.6–17.9 km;  $n$  = 38; SD = 3.1). Approximately 66% of bears located dens across years within the same or an adjacent valley. We also observed 4 individuals that relocated to new dens during winter. One bear changed den locations once in each of 2 years; the remaining 3 bears each changed den locations once during a single winter.

#### Discussion

Minimum convex polygon home ranges of female brown bears in this study ( $\bar{x}$  = 628 km<sup>2</sup>) were generally larger than those reported for adult female grizzly bears in North America (McLoughlin et al. 1999) but similar to interior grizzly bears in southcentral Alaska (408–549 km<sup>2</sup>; Ballard et al. 1982; Miller 1993; S.D. Miller, 1987, Susitna hydroelectric project final report, Volume VI: Black bear and brown bear, Alaska Department of Fish and Game, Anchorage, Alaska, USA). Female brown bears on the Alaska Peninsula had smaller home ranges ( $\bar{x}$  = 293 km<sup>2</sup>; Glenn and Miller 1980), and those in northwest Alaska had home ranges approximately twice as large as those in this study (Ballard et al. 1993). However, MCP estimators can be unreliable due to their sensitivity to sample size, inability to calculate multiple centers of activity, and sensitivity to outliers

(Seaman et al. 1999). Thus, comparisons should be made with caution.

In our study, one exceptional individual (Bear 152) had a home range whose 95% kernel estimate ( $h_{1scv}$ ) was over 8 times the size of the individual with the next largest home range (5,208 km<sup>2</sup> versus 623 km<sup>2</sup>, respectively). Similar to individuals described by Ballard et al. (1993), Bear 152's denning area was largely outside the area where she normally concentrated her activities. We also suspect we only documented the extreme movements by this extraordinarily far-ranging individual during telemetry flights; her actual movements between seasonal core areas were only occasionally determined and could only be inferred. The lower  $h$ -value ( $h_{pi}$ ) used appeared to more accurately describe the home range for Bear 152. A small value of  $h$  shows the fine detail of data in the kernel density estimate, while a large  $h$ -value obscures those features; an estimate between these extremes should be selected (Worton 1995).

Unique individuals such as Bear 152 illustrated limits of typical telemetry tracking studies, which often are unable to clearly define extensive movements. Although not as unusual as Bear 152, relocations of 3 additional bears (Bears 100, 105, and 154) also suggested occasional long-distance movements. In the cases of Bears' 100 and 105, who lived and traveled near each other, we suspected we only relocated these individuals returning to the study area from occasional long-distance movements and were unable to document the furthest extents of their ranges. One solution to this problem would have been to decrease time between relocations; however, given the logistics of this remote study area, this was not an option. Although not available at the beginning of this study, a second solution would be GPS transmitters. The higher costs of GPS transmitters can limit the number of animals studied; researchers must weigh merits of obtaining larger, unbiased samples versus using a larger group of animals with less quality data (Arthur and Schwartz 1999).

Seasonal changes in elevational use, presumably in response to available food items, denning sites, and other factors, have been noted by others (Craighead 1976, Glenn and Miller 1980, Ballard et al. 1993). Radiomarked female bears were found at lower elevations when chinook, chum, and sockeye salmon were available, then moved to higher elevations in the fall, presumably to feed on berries and ground squirrels (*Spermophilus parryii*). Caribou (*Rangifer tarandus*) were usually in the study area during late summer in higher numbers at intermediate and higher elevations (personal observation). We observed annual changes in

elevational use, also presumably in response to changing resources. One influence may have been the number of summering caribou, which became increasingly variable as the study progressed (Hinkes et al. 2005). Reproductive status apparently further influenced elevational use; females with cubs were found at higher elevations during the non-denning period. This difference may be related to females with cubs avoiding habitats frequented by adult males that may prey on the young (Pearson 1975, Ballard et al. 1993, Van Daele et al. 2001).

The distances of relocated study bears to nearest anadromous fish streams were shortest when chinook, chum, and sockeye salmon runs were at their peak (16 Jul–15 Aug). Distances from anadromous streams were farther between 16 August–15 September, coinciding with increasing berry and caribou availability. This also suggests that radiomarked bears were not returning to streams to feed on coho salmon in late August and early September.

Beginning in 1998, chinook and chum salmon escapement in Kuskokwim River drainages were low. Poor ocean survival was also noted for both species from 1998 to 2001, although less so in 2001 (Burkey et al. 2002). Radiomarked bears maintained greater average distances from anadromous streams in years when salmon escapement was low (Fig. 4). Salmon are relatively high in energy, highly digestible (Bunnell and Hamilton 1983, Pritchard and Robbins 1990), and often sufficiently aggregated that foraging efficiency is thought to not limit intake rates (Gende et al. 2001). However, brown bears most likely change their diet both seasonally (MacHutchon and Wellwood 2003) and over time, based on trade-off between food quality and digestibility as well as availability and handling time. This appeared to be the case in this study as bears apparently did not return to streams to feed on coho salmon in the fall. We suspect that when salmon escapement was low, pursuing the less abundant resource became too energetically costly and bears shifted foraging activities away from salmon streams toward habitat with presumably more accessible resources.

Successive dens of individual brown bears tend to be in the same general area but rarely in the same den structure; mean distances varied from 1.7–8.8 km with a few individuals moving up to 30 km (Linnell et al. 2000). These results coincide with our findings; however, we documented one individual that moved 37 km between consecutive dens. For Alaska, mean distances between consecutive dens in our study were larger than those on Kodiak Island (Van Daele et al. 1990) and in

southeast Alaska (Schoen et al. 1987), smaller than those in southcentral Alaska (Miller 1990), and similar to those observed in northwest Alaska (Ballard et al. 1993). We also observed 4 individuals that relocated dens during a single winter. Use of multiple den sites does not conform to the conventional denning pattern of entering a single den and remaining throughout the winter (Van Daele et al. 1990).

## Conclusions

Female home ranges in this study were large, but comparable to those noted in interior Alaskan populations, suggesting habitat similarities to areas with little access to salmon resources. Further, bears in the area exhibited characteristics (color, size, and behavior) that suggested the population was a mixing area for coastal brown bears and interior grizzly bears (Van Daele et al. 2001). The study area was beyond tree line and typical of much of western Alaska. There was a short growing season and limited food resources compared with more productive coastal areas. Although the study area was at the fringe of salmon availability, salmon influenced bear seasonal movements and distribution. Hilderbrand et al. (1999) reported that adult female body mass, mean litter size, and density of brown bear populations were related to salmon consumption. Populations of brown bears without access to salmon have lower body weights, produce smaller litters, and occur at lower population densities than populations with access to salmon (Miller et al. 1997, Hilderbrand et al. 1999). We suspect that with reduced salmon resources, our study area would support a lower bear density. Indeed, we observed population growth during the first half of the study (1993–97) and a declining population growth rate in concurrence with reduced salmon escapement (1998–2002; Kovach et al. 2006). In much of their historic range, salmon remain heavily harvested through sport-fishing, commercial fishing, and subsistence use. However, escapement goals do not typically consider wildlife and ecosystem requirements (Hilderbrand et al. 2004). We agree with others (Barnes 1990, Hilderbrand et al. 2004) that key brown bear management elements should include salmon escapement goals with an allocation of fish for brown bears in important watersheds.

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## Literature cited

- ALASKA DEPARTMENT OF FISH AND GAME. 2002. Draft 2002 Anadromous fish streams—western region. Alaska Department of Fish and Game, Habitat and Restoration Division, Anchorage, Alaska, USA.
- ARTHUR, S.M., AND C.C. SCHWARTZ. 1999. Effects of sample size on accuracy and precision of brown bear home range models. *Ursus* 11:139–148.
- BALLARD, W.B., S.D. MILLER, AND T.H. SPRAKER. 1982. Home range, daily movements, and reproductive biology of brown bears in southcentral Alaska. *Canadian Field-Naturalist* 96:1–5.
- , L.A. AYRES, D.J. REED, S.G. FANCY, AND K.E. RONEY. 1993. Demography of grizzly bears in relation to hunting and mining development in northwestern Alaska. *Scientific Monograph NPS/NRRO/NRSM* 23:1–112.
- BARNES, V.G. 1990. The influence of salmon availability on movements and range of brown bears on southwest Kodiak Island. *International Conference on Bear Research and Management* 8:305–313.
- 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.
- BERNS, V.D., G.C. ATWELL, AND D.L. BOONE. 1980. Brown bear movements and habitat use at Karluk Lake, Kodiak Island. *International Conference on Bear Research and Management* 4:293–296.
- BLUNDELL, G.M., J.A.K. MAIER, AND E.M. DEBEVEC. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs* 71:469–489.
- BUNNELL, F.L., AND T. HAMILTON. 1983. Forage digestibility and fitness in grizzly bears. *International Conference on Bear Research and Management* 5:179–185.

- BURKEY, C., JR., M. COFFING, J. ESTENSEN, R.L. FISHER, AND D.B. MOLYNEAUX. 2002. Annual management report for the subsistence and commercial fisheries of the Kuskokwim Area. Regional Information Report 3A02-53. Alaska Department of Fish and Game, Division of Commercial Fisheries, Anchorage, Alaska, USA.
- CRAIGHEAD, F.C., JR. 1976. Grizzly bear ranges and movement as determined by radiotracking. Pages 97–109 in M.R. Pelton, J.W. Lentfer, and G.E. Folk, Jr., editors. Bears—their biology and management. IUCN Publication New Serial 40.
- GENDE, S.M., T.P. QUINN, AND M.F. WILSON. 2001. Consumption choice by bears feeding on salmon. *Oecologia* 127: 372–382.
- GLENN, L.P., AND L.H. MILLER. 1980. Seasonal movements of an Alaska Peninsula brown bear population. *International Conference on Bear Research and Management* 4:307–312.
- HAMILTON, A.N., AND F.L. BUNNELL. 1987. Foraging strategies of coastal grizzly bears in the Kimsquit River valley, British Columbia. *International Conference on Bear Research and Management* 7:187–197.
- HARRIS, S., W.J. CRESSWELL, P.G. FORDE, W.J. TREWHELLA, T. WOOLLARD, AND S. WRAY. 1990. Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* 20:97–123.
- HILDERBRAND, G.V., T.A. HANLEY, C.T. ROBBINS, AND C.C. SCHWARTZ. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* 121:546–550.
- , S.D. FARLEY, C.C. SCHWARTZ, AND C.T. ROBBINS. 2004. Importance of salmon to wildlife: implications for integrated management. *Ursus* 15:1–9.
- HINKES, M.T., G.H. COLLINS, L.J. VAN DAELE, S.D. KOVACH, A.R. ADERMAN, J.D. WOOLINGTON, AND R.J. SEAVOY. 2005. Influence of population growth on caribou herd identity, calving ground fidelity, and behavior. *Journal of Wildlife Management* 69:in press.
- HOOGE, P.N., W. EICHENLAUB, AND E. SOLOMON. 1999. The animal movement program. Alaska Biological Science Center, US Geological Survey, Anchorage, Alaska, USA.
- INTERAGENCY GRIZZLY BEAR COMMITTEE. 1987. Grizzly bear compendium. National Wildlife Federation, Washington DC, USA.
- KERNOHAN, B.J., R.A. GITZEN, AND J.J. MILLSPAUGH. 2001. Analysis of animal space use and movements. Pages 125–166 in J.J. Millspaugh and J.M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.
- KOVACH, S.D. 1997. Kuskokwim Mountains brown bear capture. Report. US Fish and Wildlife Service, Yukon Delta National Wildlife Refuge, Bethel, Alaska, USA.
- . 2001. Southwest Kuskokwim Mountains brown bear and caribou capture. Report. US Fish and Wildlife Service, Yukon Delta National Wildlife Refuge, Bethel, Alaska, USA.
- . 2003. Southwest Kuskokwim Mountains brown bear capture. Report. US Fish and Wildlife Service, Yukon Delta National Wildlife Refuge, Bethel, Alaska, USA.
- , G.H. COLLINS, M.T. HINKES, AND J.W. DENTON. 2006. Reproduction and survival of brown bears in southwest Alaska. *Ursus* 17: in press.
- LINNELL, J.D.C., J.E. SWENSON, R. ANDERSON, AND B. BARNES. 2000. How vulnerable are denning bears to disturbance? *Wildlife Society Bulletin* 28:400–413.
- MACHUTCHON, A.G., AND D.W. WELLWOOD. 2003. Grizzly food habits in the northern Yukon, Canada. *Ursus* 14:225–235.
- MARROW, J.E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publishing, Anchorage, Alaska, USA.
- MATSON, G., L. VAN DAELE, E. GOODWIN, L. AUMILLER, H. REYNOLDS, AND H. HRISTIENKO. 1993. A laboratory manual for cementum age determination of Alaska brown bear first premolar teeth. Alaska Department of Fish and Game, Anchorage, Alaska, USA and Matson's Laboratory, Milltown, Montana, USA.
- McLOUGHLIN, P.D., R.L. CASE, R.J. GAU, S.H. FERGUSON, AND F. MESSIER. 1999. Annual and seasonal movement patterns of barren-ground grizzly bears in the central northwest territories. *Ursus* 11:79–86.
- MILLER, G., J. DENTON, D. FISHER, M. HINKES, R. KAYCON, S. KOVACH, S. MILLER, J. MORGART, AND L.J. VAN DAELE. 1995. Brown bear density, movements, and population parameters in the southwestern end of the Kuskokwim Mountains and adjacent ranges, western Alaska—1993 progress report. Report. US Fish and Wildlife Service, Yukon Delta National Wildlife Refuge, Bethel, Alaska, USA.
- MILLER, S.D. 1990. Denning ecology of brown bears in southcentral Alaska and comparisons with a sympatric black bear population. *International Conference on Bear Research and Management* 8:279–287.
- . 1993. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Game Management Unit 13. Federal Aid in Wildlife Restoration Project W-22-6, W-23-1, W-23-2, W-23-3, W-23-4, and W-23-5. Alaska Department of Fish and Game, Anchorage, Alaska, USA.
- , G.C. WHITE, R.A. SELLERS, H.V. REYNOLDS, J.W. SCHOEN, K. TITUS, V.G. BARNES JR., R.B. SMITH, R.R. NELSON, W.B. BALLARD, AND C.C. SCHWARTZ. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark–resight techniques. *Wildlife Monograph* 133.
- NAGY, J.A., AND M.A. HAROLDSON. 1990. Comparisons of some home range and population parameters among four grizzly bear populations in Canada. *International Conference on Bear Research and Management* 8:227–235.
- PEARSON, A.M. 1975. The northern interior grizzly bear (*Ursus arctos* L.). Canadian Wildlife Service Report Series 34. Ottawa, Ontario, Canada.

- POWELL, R.A. 2000. Animal home ranges and territories and home range estimators. Pages 65–110 in L. Boitani and T.K. Fuller, editors. *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York, New York, USA.
- PRITCHARD, G.T., AND C.T. ROBBINS. 1990. Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology* 68:1645–1651.
- SCHOEN, J., J.W. LENTFER, AND L. BEIER. 1986. Differential distribution of brown bears on Admiralty Island, southeast Alaska: a preliminary assessment. *International Conference on Bear Research and Management* 6:1–5.
- , L.V. BEIER, J.W. LENTFER, AND L.J. JOHNSON. 1987. Denning ecology of brown bears on Admiralty and Chichagof Islands. *International Conference on Bear Research and Management* 7:293–304.
- SEAMAN, D.E., AND R.A. POWELL. 1990. Identifying patterns and intensity of home range use. *International Conference on Bear Research and Management* 8:243–249.
- , 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. RAEDEKE, AND R.A. GITZEN. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- STEEL, G.D., J.H. TORRIE, AND D.A. DICKEY. 1997. *Procedures and principles of statistics: A biometrical approach*. Third edition. McGraw-Hill, New York, New York, USA.
- TAYLOR, W.P., JR., 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.
- VAN DAELE, L.J., V.G. BARNES, AND R.B. SMITH. 1990. Denning characteristics of brown bears on Kodiak Island, Alaska. *International Conference on Bear Research and Management* 8:257–267.
- , J.R. MORGART, M.T. HINKES, S.D. KOVACH, J.W. DENTON, AND R.H. KAYCON. 2001. Grizzlies, eskimos, and biologists: Cross-cultural bear management in southwest Alaska. *Ursus* 12:141–152.
- WORTON, B.J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59:794–800.

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