

Ecological flexibility of brown bears on Kodiak Island, Alaska

Lawrence J. Van Daele^{1,4}, Victor G. Barnes, Jr.², and Jerrold L. Belant³

¹Alaska Department of Fish and Game, 211 Mission Road, Kodiak, AK 99615, USA

²PO Box 1546, Westcliffe, CO 81252, USA

³Carnivore Ecology Laboratory, Forest and Wildlife Research Center, Mississippi State University, Box 9690, Mississippi State, MS 39762, USA

Abstract: Brown bears (*Ursus arctos*) are a long-lived and widely distributed species that occupy diverse habitats, suggesting ecological flexibility. Although inferred for numerous species, ecological flexibility has rarely been empirically tested against biological outcomes from varying resource use. Ecological flexibility assumes species adaptability and long-term persistence across a wide range of environmental conditions. We investigated variation in population-level, coarse-scale resource use metrics (i.e., habitat, space, and food abundance) in relation to indices of fitness (i.e., reproduction and recruitment) for brown bears on Kodiak Island, Alaska, 1982–97. We captured and radiocollared 143 females in 4 spatially-distinct segments of this geographically-closed population, and obtained ≥ 30 relocations/individual to estimate multi-annual home range and habitat use. We suggest that space use, as indexed using 95% fixed kernel home ranges, varied among study areas in response to the disparate distribution and abundance of food resources. Similarly, habitat use differed among study areas, likely a consequence of site-specific habitat and food (e.g. berries) availability. Mean annual abundance and biomass of spawning salmon (*Oncorhynchus* spp.) varied >15 -fold among study areas. Although bear use of habitat and space varied considerably, as did availability of dominant foods, measures of fitness were similar (range of mean litter sizes = 2.3–2.5; range of mean number of young weaned = 2.0–2.4) across study areas and a broad range of resource conditions. Our data support the thesis that brown bears on Kodiak Island display ecological flexibility. This adaptability is likely representative of the entire species and has helped facilitate its wide geographic distribution and abundance. We suggest variation in brown bear resource use necessitates area-specific management strategies to ensure suitable conditions for their long-term persistence.

Key words: Alaska, biological outcome, brown bear, ecological flexibility, fitness, habitat use, home range, Kodiak Island, *Ursus arctos*

Ursus 23(1):21–29 (2012)

Ecological flexibility assumes adaptability and long-term persistence of a species across a wide range of environmental conditions. Species that can exist in diverse ecosystems or habitats have the potential to occupy larger areas and maintain higher population densities (Hutchinson 1957). Although inferred for numerous species across diverse taxa (e.g., Nentwig et al. 2009, Hoffman and O’Riain 2011), ecological flexibility has rarely been empirically tested against biological outcomes from varying resource use (but see Lahann and Dausmann 2011). Ecological flexibility is in part a consequence of animal behavior, with individuals making decisions

that result in positive or negative outcomes (Blumstein and Bouskila 1996). These outcomes can range from minor (e.g., flight response from a predator) to severe (e.g., death). Many of these outcomes are measurable, and vary from cortisol levels to assess short-term or chronic stress, to estimates of survival and cause-specific mortality. Knowing the biological outcomes of resource use can be useful in assessing population-level effects in relation to resources used, and can potentially help guide management activities. Additionally, ecological flexibility of individuals or species can be constrained by extrinsic factors (e.g., weather, conspecifics) that can influence resource use at the individual (e.g., access to food source) or species level (e.g., geographic range). Constraints on animal

⁴larry.vandaele@alaska.gov

resource use can include resource competition, social rank, environmental conditions, and anthropogenic disturbances (Millsbaugh et al. 2001, Van Meter et al. 2009). Thus, ecological flexibility is associated with an individual's or species' realized niche or area occupied (Hutchinson 1957). Constraints on individual or sex-age classes of brown bears (*Ursus arctos*) include conspecific exclusion from high-quality foraging sites (e.g., salmon [*Oncorhynchus* spp.] streams [Ben-David et al. 2004, McLellan 2005]) and denning areas (Libal et al. 2011).

Brown bears are a long-lived species that demonstrate considerable individual variation (Gillies et al. 2006, Edwards et al. 2011). Although purportedly better adapted to exploit more open areas (Herrero 1978), brown bears have been or are currently distributed across most terrestrial ecoregions in the Holarctic Realm (Servheen et al. 1999, Schwartz et al. 2003, Davison et al. 2010). Brown bears occupy and use a wide variety of habitats (e.g., Belant et al. 2010, Roever et al. 2010) and food types (e.g., Hilderbrand et al. 1999, Belant et al. 2006, Edwards et al. 2011). Consequently, brown bears appear to exhibit ecological flexibility; however, no quantitative assessment of this concept has been conducted.

To investigate ecological flexibility of brown bears, we opportunistically used data from 4 studies conducted across Kodiak Island from 1982–97. These studies involved a geographically-closed population (Talbot et al. 2006) with no physical barriers to brown bear movement. Our objective was to assess if variation in population-level resource use and abundance (e.g., home range, habitat use, and food abundance) among study populations occurred, and if observed variation in resource use influenced biological outcomes (i.e., reproduction and recruitment). We hypothesized that bears could successfully occupy any habitat matrix on Kodiak Island without adversely affecting biological outcomes. Support for this hypothesis would demonstrate ecological flexibility by brown bears and necessitate localized management of suitable resources. Rejection of this hypothesis would suggest a narrower range of suitable ecological conditions that could potentially be used to identify important habitats for management.

Study area

Kodiak Island is in the western Gulf of Alaska (56°45'–58°00'N, 152°09'–154°47'W; Fig. 1), comprises 8,975 km², and supports about 3,500 brown

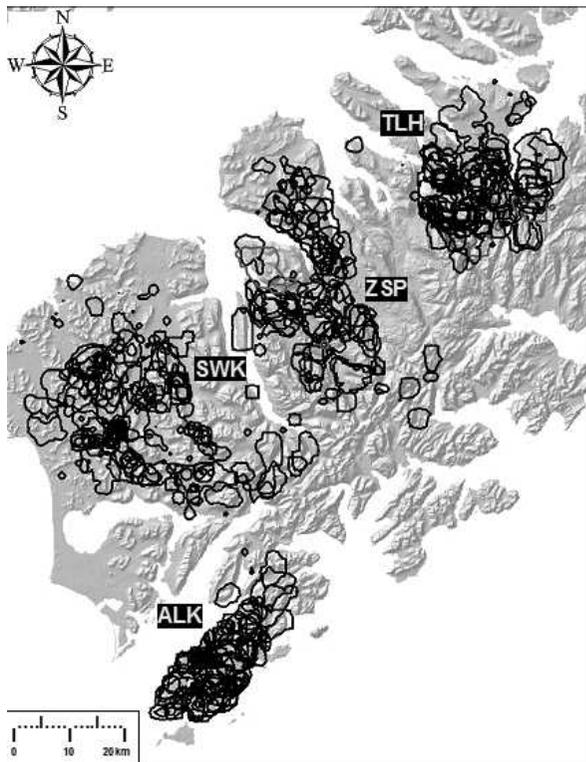


Fig. 1. Brown bear study areas (TLH = Terror Lake, ZSP = Zachar/Spiridon, SWK = southwest Kodiak, and ALK = Aliulik Peninsula) and 95% fixed kernel home ranges for female brown bears with ≥ 30 relocations, Kodiak Island, Alaska, 1982–97.

bears (Van Daele 2007). The climate is sub-arctic maritime, with variable weather due to topographic relief. The south and west sides of Kodiak Island have a drier climate due to prevailing weather and a mountain range with elevations to 1,362 m that divides the island.

A detailed description of Kodiak Island vegetation is provided by Fleming and Spencer (2004). Sitka spruce (*Picea sitchensis*) is common on northeastern Kodiak Island with devil's club (*Echinopanax horridum*), high-bush blueberry (*Vaccinium ovalifolium*), and bracken fern (*Dryopteris dilatata*) the principal understory vegetation in forested areas. Shrub–grass–forb complexes occur throughout lowland (<150 m) and mid-elevation (150–500 m) areas. Representative species are Sitka alder (*Alnus crispa sinuata*), willows (*Salix* spp.), Kenai birch (*Betula kenaica*), European red elder (*Sambucus racemosa*), salmonberry (*Rubus spectabilis*), red-topped grass (*Calamagrostis canadensis*), fireweed (*Epilobium angustifolium*), and cow

parsnip (*Heracleum lanatum*). Cottonwood trees (*Populus balsamifera*) and willow communities are typical along streams. On southwestern Kodiak Island, extensive areas of regularly-spaced hummocks (0.3–1.0 m tall) and moist tundra are common.

Alpine vegetation (>500 m elevation) consists of mixtures of low willow, sedge (*Carex macrocheata*), crowberry (*Empetrum nigrum*), low-bush cranberry (*Oxycoccus microcarpus*), alpine blueberry (*Vaccinium uliginosum*), and various forbs. Nearshore waters support abundant marine vegetation, including bull kelp (*Nereocystis luetkeana*), eelgrass (*Zostera marina*), and bladderwrack (*Fucus gardneri*), with tidal action and storms often depositing these plants on shore. Shoreline vegetation includes goose tongue (*Plantago maritima*), beach greens (*Honckenya pelloides*), and beach rye (*Elymus arenarius*).

Willson and Halupka (1995) noted that salmon were keystone species in many coastal terrestrial ecosystems along the Pacific Rim and provide an influx of marine nutrients (Hilderbrand and Robbins 1999, Quinn et al. 2009). Kodiak Island's lakes and streams provide important habitat for 5 species of Pacific salmon (*Oncorhynchus* spp.), steelhead (*O. mykiss*), arctic char (*Salvelinus alpinus*), and Dolly Varden (*S. malma*). Importance of spawning salmon to brown bear abundance and condition is well established (Hilderbrand et al. 1999, Belant et al. 2006).

Methods

Our data were derived from 4 brown bear research projects on Kodiak Island that used radio telemetry (Fig. 1) to address specific management questions. The Terror Lake hydroelectric investigation (1982–94) assessed potential bear response to a proposed hydroelectric facility (Smith and Van Daele 1990). The Zachar/Spiridon study (1988–97) investigated relationships between bears and deer (*Odocoileus hemionus*) hunters during a period of increasing bear–deer hunter encounters (Barnes 1994). The Southwest Kodiak study (1983–94) assessed annual-use patterns of salmon spawning areas by bears and explored the possibility of developing methods to estimate population trends (Barnes 1990). The Aliulik Peninsula research project (1992–97) investigated population dynamics of bears living in tundra–heath habitat (Barnes and Smith 1997). Radio telemetry work was extended through 1997 on all study areas to acquire long-term reproductive data

and to obtain population density estimates (Miller et al. 1997, Barnes and Smith 1998, Barnes and Van Daele 2008).

We used comparable capture, handling, and processing techniques in all investigations. Female bears were captured in late spring or early summer by chemically immobilizing them with Etorphine (M99[®], Lemmon Pharmaceutical, Sellersville, Pennsylvania, USA) or tiletamine hydrochloride and zolazepam hydrochloride (Telazol[®], Fort Dodge Laboratories, Fort Dodge, Iowa, USA). Drugs were administered from darts fired from Palmer capture equipment (Palmer Cap-Chur, Powder Springs, Georgia, USA) by biologists in small helicopters (Bell 206 or Hughes 500). Immobilization dosages were typically 5 ml for subadults and 7 ml for adults (Etorphine: 1.0 mg/ml; Telazol: 200 mg/ml). Bears immobilized with Etorphine were administered dipenorphine as a reversal agent (2.0 mg/ml; M50-50[®], Lemmon Pharmaceutical, Sellersville, Pennsylvania, USA); no antagonist was used with Telazol.

For each captured female we recorded reproductive status and extracted a first premolar tooth for aging using cementum annuli counts (Matson et al. 1993). Tattoos were applied to the inside of the lips or groin; numbered plastic tags were affixed to each ear. We deployed conventional VHF radio-collar transmitters (Telonics Inc., Mesa, Arizona, USA) on a sample of female bears in each study area and recaptured bears every 2–3 years to replace transmitters.

Collared bears were typically relocated from fixed-winged aircraft (Piper PA-18 or equivalent) weekly, but inclement weather commonly reduced flight frequency. We reduced the flight schedule to twice monthly during winter. Tracking flight frequency was increased to at least weekly during spring emergence to estimate cub production and survival. During each flight, we attempted to locate all collared bears and recorded locations on 1:63,360 US Geological Survey topographic maps that were later digitized to obtain coordinates. Our telemetry relocations were collected only during daylight and favorable flying conditions, so were not a complete or unbiased sample of habitat use by individual bears (Belant and Follmann 2002, Moe et al. 2007). However, they likely provided a reasonable estimate of overall home range size (Demma and Mech 2011). We included winter relocations, including den locations, because reduced winter flight schedules (1–2 times/month) coupled with periodic winter activity and multiple den use reduced potential

problems with autocorrelation. Additionally, any potential bias in home range estimates was similar among individuals and across study areas.

We analyzed relocation data to determine sample size necessary for multi-annual home range estimation (Seaman et al. 1999). We conducted our initial analysis on bears relocated ≥ 100 times ($n = 60$ females), assuming home ranges at that sample size represented the actual home range (Belant and Follmann 2002). We calculated the percentage of home ranges of female bears represented by each iteration of 10 serial relocations (e.g., 10, 20, 30, etc.) and determined that home ranges reached 100% levels (SE = 4%) with 30 relocations. We then calculated multi-annual 95% fixed kernel home range estimates using least squares cross validation with a minimum window of 500 m (Worton 1989) for each bear with ≥ 30 locations using BIOTAS software (Ecological Software Solutions, Hegymagas, Hungary). We compared female home range sizes among study areas using general linear models (GLM; SAS version 9.1, SAS Institute Inc., Cary, North Carolina, USA). A Tukey test was used for multiple comparisons; mean values are reported with 1 SE.

We used ArcView 9.1 GIS software (Environmental Systems Research Institute, Redlands, California, USA) and a vegetative cover map for the Kodiak Archipelago (Fleming and Spencer 2004) to assess habitat use (excluding marine waters). We consolidated the 64 distinct cover types of Fleming and Spencer (2004) into 8 categories that reflected unique cover and feeding opportunities for bears (rock-ice, alpine, tall shrub, low shrub, grassland, heath, wetlands, and freshwater; Van Daele 2007). Overall percentages of these 8 habitat categories on Kodiak Island were: rock-ice (9.1%), alpine (17.0%), tall shrub (46.6%), low shrub (7.8%), grassland (8.8%), heath (4.7%), wetlands (4.3%), and freshwater (1.7%). We collectively analyzed data from all bears within each study to estimate population-level habitat use. We summed the area of each cover type contained within the home range of individual bears and converted these to percentages of individual home ranges. We then compared mean percentages of habitats used by bears across study areas using GLM with Tukey tests. Thus, we did not directly assess habitat selection but rather habitat use because we assumed the comparatively small size of Kodiak Island provided bears potential access to any area within the island. Brown bears can travel considerable distances, sometimes exceeding 80 km

for short-term or seasonal movements (Mertzanis et al. 2005, Krofel et al. 2010, J.L. Belant unpublished data). Furthermore, it is unnecessary to estimate selection to understand biological responses (e.g., reproduction) in relation to resource use because selection does not cause the observed biological responses.

We calculated mean annual salmon biomass and availability to bears in each study area derived from Alaska Department of Fish and Game (ADF&G) weir counts, aerial surveys, and field estimates during the study period (Kuriscak 2004; ADF&G unpublished data, Kodiak, Alaska). We used ANOVA and a Tukey test to compare mean salmon abundance across study areas.

Finally, we compared attributes of resource use and food availability among study populations to estimates of reproduction for these same populations (Barnes and Van Daele 2008). Specifically, we assessed whether mean cub litter size and mean number of young weaned/female varied among study areas in response to resource use.

Results

We captured and radiocollared 196 independent female brown bears, including 143 individuals with ≥ 30 relocations used for analyses (Terror Lake = 45, Zachar/Spiridon = 37, Southwest Kodiak = 33, and Aliulik Peninsula = 28). Mean 95% fixed kernel home range of all female bears was 50.1 km² (SE = 1.9; Table 1). Mean home range size varied across study areas ($F = 5.18$; 3, 140 df; $P = 0.002$) with home ranges larger ($P < 0.05$) in Aliulik Peninsula than in Terror Lake and Zachar/Spiridon. Although considerable individual home range overlap occurred within study areas, we observed no overlap among females from different study areas (Fig. 1).

Bears used all habitats in each study area (Table 2); however, habitat use differed within ($F = 7.54$; 7, 1112 df; $P < 0.001$) and across ($F = 215.83$; 3, 1112 df; $P < 0.001$) study areas. There was also a habitat \times study area interaction ($F = 7.54$; 21, 1112 df; $P < 0.001$). Habitat use was most similar between Terror Lake and Zachar/Spiridon, with use differing ($P < 0.05$) only in amount of rock-ice habitat. In contrast, habitat use was least similar between Terror Lake and Aliulik Peninsula, with use similar ($P > 0.05$) only for freshwater habitat.

Mean annual number and available biomass of spawning salmon varied more than 15-fold among

Table 1. Mean and standard error (SE) for 95% fixed kernel home range (≥ 30 relocations/animal) sizes and reproductive parameters for female brown bears, Kodiak Island, Alaska, 1982–97. Column means with different letters are significantly different ($P > 0.05$).

Study area	Home range (km ²)				Reproduction ^a					
	n	Mean	SE	Range	Initial litter size			Number weaned		
					n	Mean	SE	n	Mean	SE
Terror Lake	45	45.1a	2.5	23.5–98.5	77	2.5a	0.1	56	2.0a	0.1
Zachar/Spiridon	37	43.8a	3.2	16.3–119.1	56	2.3a	0.1	39	2.1a	0.1
Southwest Kodiak	33	54.3ab	4.9	20.5–165.0	53	2.4a	0.1	50	2.0a	0.1
Aliulik Peninsula	28	61.7b	4.2	29.6–115.5	16	2.5a	0.2	16	2.4a	0.2
Combined	143	50.1	1.9	16.3–165.0	202	2.4	0.1	161	2.0	0.1

^aFrom Barnes and Van Daele (2008)

study areas, with lowest numbers and biomass in Terror Lake and highest abundance and biomass in Southwest Kodiak (Table 3). Duration of combined peak salmon runs varied almost 3-fold, ranging from 44 days for Aliulik Peninsula, 53 days for Zachar/Spiridon, 93 days for Terror Lake, to 118 days for Southwest Kodiak.

Mean litter size of cubs-of-the-year during May was similar ($P > 0.05$) across study areas (range = 2.3–2.5) as was mean number of young weaned/female (range = 2.0–2.4; Table 1).

Discussion

We documented variation in space and habitat use by female brown bears across Kodiak Island with markedly different abundances of high-quality food, especially salmon. That corresponding indices of fitness among population segments, as measured by initial litter sizes and numbers of young weaned, were similar supports ecological flexibility of brown bears within the range of resource conditions investigated. Brown bears have persisted across a large geographic range (Schwartz et al. 2003,

Davison et al. 2010) and use diverse habitats (Belant et al. 2010, Roever et al. 2010), further supporting ecological flexibility.

We suggest that observed variation in home range and habitat use largely reflected quality and availability of food. For example, bears with largest home ranges occurred on the Aliulik Peninsula, an area with few concentrated food sources. Salmon availability was comparatively limited and of short duration, and berries and sedges were seasonally abundant but widely dispersed. Bears on the Aliulik Peninsula also used windrowed marine detritus; the importance of intertidal foraging by brown bears has been demonstrated (Smith and Partridge 2004). Intertidal foraging provided bears with emergent coastal vegetation in spring and early summer, and occasional large sources of meat including dead gray (*Eschrichtius robustus*), humpback (*Megaptera novaeangliae*), and fin (*Balaenoptera physalus*) whales that washed ashore, and deer that died during winter. Marine detritus also harbored invertebrates, including beach hoppers (*Traskorchestia traskiana*) and insect larvae. Myrmecophagy is seasonally important for some brown bear populations in

Table 2. Mean annual habitat use of female brown bears by study area, Kodiak Island, Alaska, 1982–97. Row means with different letters are significantly different ($P < 0.05$).

Habitat	Habitat use (km ²)							
	Terror Lake (n = 45)		Zachar/Spiridon (n = 37)		Southwest Kodiak (n = 33)		Aliulik Peninsula (n = 28)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Rock-ice	11.80a	5.81	2.46b	0.55	1.69b	0.50	0.35b	0.04
Alpine	14.67a	7.19	9.53a	1.05	6.15b	0.80	3.03c	0.42
Tall shrub	44.16b	21.63	21.35a	1.28	24.22a	2.18	9.90b	1.39
Low shrub	6.69a	3.29	4.15a	0.60	7.03b	0.99	1.32c	0.18
Grassland	2.70a	1.33	1.74a	0.16	3.45b	0.37	11.71c	0.66
Heath	0.41a	0.20	0.16a	0.02	3.11a	0.49	21.54b	2.62
Wetlands	2.26a	1.12	1.02a	0.14	4.16b	0.73	4.83b	0.44
Freshwater	1.07a	0.53	0.88a	0.19	3.13b	0.76	0.80a	0.09

Table 3. Estimated mean annual availability of spawning salmon by study area, Kodiak Island, Alaska, 1982–97.

Study area	Species ^a	Annual escapement ^b	Available biomass (kg) ^c	Timing of runs	Peak run
Terror Lake	king (chinook)	0	0	—	—
	sockeye (red)	1,700	3,910	10 Jun–10 Aug	20 Jun–10 Jul
	chum (dog)	29,200	99,280	10 Jul–10 Sep	15 Aug–30 Aug
	pink (humpy)	141,500	212,250	15 Jul–20 Sep	10 Aug–10 Sep
	silver (coho)	9,000	32,400	15 Aug–5 Oct	15 Sep–30 Sep
	combined	181,400	347,840	10 Jun–5 Oct	01 Jul–20 Sep
Zachar/Spiridon	king (chinook)	0	0	—	—
	sockeye (red)	0	0	—	—
	chum (dog)	38,700	131,580	10 Jul–20 Sep	30 Jul–25 Aug
	pink (humpy)	130,800	196,200	10 Jul–10 Sep	10 Aug–25 Aug
	silver (coho)	15,500	55,800	15 Aug–5 Oct	15 Sep–30 Sep
	combined	185,000	383,580	10 Jul–5 Oct	30 Jul–20 Sep
Southwest Kodiak	king (chinook)	23,100	214,830	25 May–10 Jul	05 Jun–20 Jun
	sockeye (red)	1,314,800	3,024,040	25 May–01 Oct	05 Jun–20 Jun; 15 Aug–15 Sep
	chum (dog)	40,900	139,060	20 Jun–10 Sep	20 Jul–20 Aug
	pink (humpy)	1,335,200	2,002,800	10 Jul–10 Sep	1 Aug–20 Aug
	silver (coho)	73,500	264,600	15 Aug–5 Oct	15 Sep–30 Sep
	combined	2,787,500	5,645,330	25 May–5 Oct	5 Jun–25 Sep
Aliulik Peninsula	king (chinook)	0	0	—	—
	sockeye (red)	0	0	—	—
	chum (dog)	14,300	48,620	1 Aug–15 Sep	5 Aug–1 Sep
	pink (humpy)	375,800	563,700	15 Jul–10 Sep	10 Aug–30 Aug
	silver (coho)	2,000	7,200	15 Aug–5 Oct	15 Sep–30 Sep
	combined	392,100	619,520	15 Jul–5 Oct	10 Aug–1 Sep

^aKing (*Oncorhynchus tshawytscha*), sockeye (*O. nerka*), chum (*O. keta*), pink (*O. gorbuscha*), silver (*O. kisutch*)

^bMean estimates based on weir counts, aerial surveys, and field estimates (Alaska Department of Fish and Game files, Kodiak, Alaska).

^cMean weights by species: king = 9.3 kg; sockeye = 3.6 kg; chum = 3.4 kg; pink = 1.5 kg; and, silver = 3.6 kg (Alaska Department of Fish and Game, unpublished data).

North America, Scandinavia, and Japan (Swenson et al. 1999, Mattson 2001, Yamazaki et al. 2012), but ants are rare on the Kodiak Archipelago. Beach hoppers may be an ecological equivalent to ants as a food source for bears on Kodiak. Overall, we suggest seasonally available and dispersed food sources on Aliulik Peninsula resulted in larger observed home ranges.

Contrary to our expectations, home range size in Southwest Kodiak, where salmon were most abundant, was similar to home range size in other areas of the island. We expected smaller mean home range size in Southwest Kodiak because salmon abundance has been shown to be positively correlated with brown bear population density (Hilderbrand et al. 1999). Further, smaller home range size suggests reduced movements, which in turn reduces energy expenditures and can improve fitness, an expected outcome of high food abundance. We observed many bears in Southwest Kodiak using streams with spawning salmon as fish arrived and then moving

to other streams as salmon abundance decreased (Barnes 1990). This pattern may also have been influenced by use of fresh salmon when available, because salmon have higher lipid and protein levels when they enter spawning streams (Gende et al. 2004). Elderberries (*Sambucus* spp.) were also seasonally abundant near salmon spawning areas and in areas of low shrub habitat on Southwest Kodiak. Welch et al. (1997) reported brown bears selected berry-producing plants with clusters or high abundance of fruit that permitted large bite sizes or high bite rates, such as elderberry. Although berries have a lower nutritional value than salmon and are less efficient to consume, Rode and Robbins (2000) found that a mixed diet of salmon and fruit enhanced weight gain more than salmon or fruit diets alone. Use of multiple and dispersed salmon spawning areas and low shrub habitat to achieve a mixed diet of fruit and salmon may explain comparable home range size of bears in Southwest Kodiak to other areas of the island.

The importance of salmon to brown bear diets is well documented (Hilderbrand et al. 1999). Brown bears on Kenai Peninsula, Alaska, slightly smaller than brown bears on Kodiak Island, required 1,003 kg salmon/bear/yr to maintain body condition (Hilderbrand et al. 2004). Using brown bear density estimates from our study areas of 200–221 independent bears/1,000 km² (Barnes and Smith 1998, Van Daele 2007), bears had access to an average of 3,893 kg salmon/yr (range = 1,482 kg salmon in Zachar/Spiridon to 13,976 kg salmon in Southwest Kodiak). It seems plausible that bears on all Kodiak study areas had access to adequate salmon biomass to meet dietary requirements. We suggest that overall abundance of marine and terrestrial meat and herbaceous foods resulted in comparable high densities island-wide (\bar{x} = 214.4 independent bears/1,000 km²; Van Daele 2007). McLoughlin et al. (2000) suggested that high habitat quality results in small home range sizes with extensive overlap across individuals. This is consistent with our findings, as home ranges on Kodiak were generally small compared to previous studies (see review by Dahle and Swenson 2003), with considerable home range overlap observed in all study areas.

Management implications

Ecological flexibility of the Kodiak brown bear population has allowed population expansion to all available habitats, increasing carrying capacity over that expected if bears conformed to uniform habitat use. Further, overall apparent high availability of nutritious food contributed to high quality bear habitat. In areas with high bear densities such as Kodiak Island, unoccupied areas of suitable habitat appear limited, suggesting some management actions (e.g., translocation) should be used with caution. Highly variable resource use among brown bear population segments demonstrates the difficulty in making management decisions based on site-specific knowledge of this species. Differential resource use can be expected to result in varying population responses to current management or environmental conditions (e.g., climate change). Generalist life history traits of brown bears indicate the need for site-specific management on Kodiak Island.

Acknowledgments

Completion of this project required the assistance of scores of dedicated professionals and interested

individuals, and we are deeply indebted to all of them. Primarily, we acknowledge the efforts of our colleague, R. Smith, who shared responsibility as a project leader on the 4 research projects used for this analysis. Among others who contributed, we especially thank the following who assisted as pilots, field workers, supervisors, administrative staff, professional advisors, editors, and fund raisers: B. Ballenger (deceased), J. Barnes, K. Becker, J. Bellinger, G. Castonguay, T. Chatto (deceased), D. Cline, J. Crye, J. Dinnocenzo, H. Downs, S. Fejes, G. Garner (deceased), E. Garton, D. Grann, E. Gunter, R. Hander, G. Hilderbrand, K. Humes, D. Johnson, A. Jones, J. Keay, B. Lofstedt, C. Lofstedt, V. Lofstedt, S. Malutin, J. Manning, D. McAllister, W. Melquist, D. Menke (deceased), D. Mensch, L. Metz, J. Miller, S. Miller, D. Minke, D. Munoz, B. Palmisano, L. Pank, J. Patterson, W. Pyle, J. Revalee (deceased), H. Reynolds, T. Richardson, M. Robus, K. Ryan, J. Sarvis, K. Schneider, R. Sellers, J. Sellinger, C. Strickland (deceased), E. Solomon, R. Strauch, H. Terry, H. Van Daele, M. Van Daele, M. Vivian, J. Want, G. Wilker (deceased), R. Wright, and D. Zweifelhofer. Funding and logistic support was provided by Alaska Department of Fish and Game, Alaska Power Authority, Kodiak Brown Bear Research and Habitat Maintenance Trust, Kodiak National Wildlife Refuge, National Fish and Wildlife Foundation, Safari Club International, US Fish and Wildlife Service (Region 6), US Geological Survey, and Wildlife Forever.

Literature cited

- BARNES, V.G., JR. 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.
- . 1994. Brown bear–human interactions associated with deer hunting on Kodiak Island. *International Conference on Bear Research and Management* 9(1):63–73.
- , AND R.B. SMITH. 1997. Population ecology of brown bears on Aliulik Peninsula, Kodiak Island, Alaska. Final Report National Fish and Wildlife Foundation, Project 94–237. US National Biological Service and Alaska Department of Fish and Game, Kodiak, Alaska, USA.
- , AND ———. 1998. Estimates of brown bear abundance on Kodiak Island, Alaska. *Ursus* 10:1–9.
- , AND L.J. VAN DAELE. 2008. Productivity of female brown bears on Kodiak Island, Alaska. Job completion

- report for Challenge Cost Share Project. Alaska Department of Fish and Game, Kodiak, Alaska, USA.
- 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.
- , K. KIELLAND, E.H. FOLLMANN, AND L.G. ADAMS. 2006. Interspecific resource partitioning in sympatric ursids. *Ecological Applications* 16:2333–2343.
- , B. GRIFFITH, Y. ZHANG, E. FOLLMANN, AND L. ADAMS. 2010. Population-level resource selection by sympatric brown and American black bears in Alaska. *Polar Biology* 33:31–40.
- BEN-DAVID, M., K. TITUS, AND L.V.R. BEIER. 2004. Consumption of salmon by Alaskan brown bears: A trade-off between nutritional requirements and the risk of infanticide? *Oecologia* 138:465–474.
- BLUMSTEIN, D.T., AND A. BOUSKILA. 1996. Assessment and decision making in animals: A mechanistic model underlying behavioral flexibility can prevent ambiguity. *Oikos* 77:569–576.
- DAHLE, B., AND J.E. SWENSON. 2003. Home ranges in adult Scandinavian brown bears (*Ursus arctos*): Effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology* 260:329–335.
- DAVISON, J., S.Y.W. HO, S.C. BRAY, M. KORSTEN, E. TAMMELEHT, M. HINDRIKSON, K. ØSTBYE, S. LAURITZEN, J. AUSTIN, A. COOPER, AND U. SAARMA. 2010. Late-quaternary biogeographic scenarios for the brown bear (*Ursus arctos*), a wild mammal model species. *Quaternary Science Reviews* 30:418–430.
- DEMMA, D.J., AND L.D. MECH. 2011. Accuracy of estimating wolf summer territories by daytime locations. *American Midland Naturalist* 165:436–445.
- EDWARDS, M.A., A.E. DEROCHE, K.A. HOBSON, M. BRANIGAN, AND J.A. NAGY. 2011. Fast carnivores and slow herbivores: Differential foraging strategies among grizzly bears in the Canadian Arctic. *Oecologia* 165: 877–889.
- FLEMING, M.D., AND P. SPENCER. 2004. A vegetative cover map for the Kodiak Archipelago, Alaska. US Geological Service, Alaska Science Center, Anchorage, Alaska, USA.
- GENDE, S.M., T.P. WUINN, R. HILLBORN, A.P. HENDRY, AND B. DICKERSON. 2004. Brown bear selectivity kill salmon with higher energy content but only in habitats that facilitate choice. *Oikos* 104:518–528.
- GILLIES, C.S., M. HEBBLEWHITE, S.E. NIELSEN, M.A. KRAWCHUK, C.L. ALDRIDGE, J.L. FRAIR, D.J. SAHER, C.E. STEVENS, AND C.L. JERDE. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887–898.
- 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, G.V., AND C.T. ROBBINS. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* 121: 546–550.
- , C.C. SCHWARTZ, C.T. ROBBINS, M.E. JACOBY, T.A. HANLEY, S.M. ARTHUR, AND C. SERVHEEN. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation on North American brown bears. *Canadian Journal of Zoology* 77:132–138.
- , S.D. FARLEY, C.C. SCHWARTZ, AND C.T. ROBBINS. 2004. Importance of salmon to wildlife: Implications for integrated management. *Ursus* 15:1–9.
- HOFFMAN, T.S., AND M.J. O'RIAIN. 2011. The spatial ecology of chacma baboons (*Papio ursinus*) in a human-modified environment. *International Journal of Primatology* 32:308–328.
- HUTCHINSON, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.
- KROFEL, M., S. FILACORDA, AND K. JERINA. 2010. Mating-related movements of male brown bears on the periphery of an expanding population. *Ursus* 21:23–29.
- KURISCAK, P. 2004. Kodiak Management Area salmon escapement daily cumulative counts for fish weirs, 1993–2002 — Regional Informational Report 4K04-38. Alaska Department of Fish and Game, Kodiak, Alaska, USA.
- LAHANN, P., AND K.H. DAUSMANN. 2011. Live fast, die young flexibility of life history traits in the fat-tailed dwarf lemur (*Cheirogaleus medius*). *Behavioral and Ecological Sociobiology* 65:381–390.
- LIBAL, N.S., J.L. BELANT, B.D. LEOPOLD, G. WANG, AND P.A. OWEN. 2011. Despotism and risk of infanticide influence grizzly bear den-site selection. *PLoS ONE* 6(9):e24133.
- 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.
- MATTSON, D.J. 2001. Myrmecophagy by Yellowstone grizzly bears. *Canadian Journal of Zoology* 79:779–793.
- MCLELLAN, B.N. 2005. Sexually selected infanticide in grizzly bears: The effects of hunting on cub survival. *Ursus* 16:141–156.
- MCLOUGHLIN, P.D., S.H. FERGUSON, AND F. MESSIER. 2000. Intraspecific variation in home range overlap with habitat quality: A comparison among brown bear populations. *Evolutionary Ecology* 14:39–60.
- MERTZANIS, Y., I. LOANNIS, A. MAVRIDIS, O. NIKOLAOU, S. RIEGLER, A. RIEGLER, AND A. TRAGOS. 2005. Movements, activity patterns and home range of a female brown bear (*Ursus arctos*, L.) in the Rodopi Mountain Range, Greece. *Belgian Journal of Zoology* 135:217–221.
- MILLER, S.D., 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 Monographs* 133.
- MILLSPAUGH, J.J., R.J. WOODS, K.E. HUNT, K.J. RAEDEKE, G.C. BRUNDIGE, B.E. WASHBURN, AND S.K. WASSER. 2001. Fecal glucocorticoid assays and the physiological stress response in elk. *Wildlife Society Bulletin* 29: 899–907.
- MOE, T.P., J. KINDBERG, I. JANSSON, AND J.E. SWENSON. 2007. The importance of diel behaviour when studying habitat selection: Examples from female Scandinavian brown bears (*Ursus arctos*). *Canadian Journal of Zoology* 85:518–525.
- NENTWIG, W., E. KÜHNEL, AND S. BACHER. 2009. A generic impact-scoring system applied to alien mammals in Europe. *Conservation Biology* 24:302–311.
- QUINN, T.P., S.M. CARLSON, S.M. GENDE, AND H.B. RICH, JR. 2009. Transportation of Pacific salmon carcasses from streams to riparian forests by bears. *Canadian Journal of Zoology* 87:195–203.
- RODE, K.D., AND C.T. ROBBINS. 2000. Why bears consume mixed diets during fruit abundance. *Canadian Journal of Zoology* 78:1640–1645.
- ROEVER, C.L., M.S. BOYCE, AND G.B. STENHOUSE. 2010. Grizzly bears and forestry. II. Grizzly bear habitat selection and conflicts with road placement. *Forest Ecology and Management* 256:1262–1269.
- SCHWARTZ, C.C., S.D. MILLER, AND M.A. HAROLDSON. 2003. Grizzly bear. Pages 556–586 in G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. *Wild mammals of North America: Biology, management, and conservation*. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- SEAMAN, D.E., 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.
- SERVHEEN, C., S. HERRERO, AND B. PEYTON. 1999. Bears status survey and conservation action plan. IUCN/SSC Bear and Polar Bear Specialist Groups, Cambridge, UK.
- SMITH, R.B., AND L.J. VAN DAELE. 1990. Impacts of hydroelectric development on brown bears, Kodiak Island, Alaska. *International Conference on Bear Research and Management* 8:93–103.
- SMITH, T.S., AND S.T. PARTRIDGE. 2004. Dynamics of intertidal foraging by coastal brown bears in southwestern Alaska. *Journal of Wildlife Management* 68:233–240.
- SWENSON, J.E., A. JANSSON, R. RIIG, AND F. SANDEGREN. 1999. Bears and ants: Myrmecophagy by brown bears in central Scandinavia. *Canadian Journal of Zoology* 77:551–561.
- TALBOT, S.L., J.R. GUST, G.K. SAGE, A. FISCHBACH, K. AMSTRUP, W. LEACOCK, AND L. VAN DAELE. 2006. Genetic characterization of brown bears of the Kodiak Archipelago. Alaska Department of Fish and Game, US Fish and Wildlife Service, and US Geological Survey, Anchorage, Alaska, USA.
- VAN DAELE, L.J. 2007. Population dynamics and management of brown bears on Kodiak Island, Alaska. Dissertation, University of Idaho, Moscow, USA.
- VAN METER, P.E., J.A. FRENCH, S.M. DLONIAK, H.E. WATTS, J.M. KOLOWSKI, AND K.E. HOLEKAMP. 2009. Fecal glucocorticoids reflect socio-ecological and anthropogenic stressors in the lives of wild spotted hyenas. *Hormones and Behavior* 55:329–337.
- WELCH, C.A., J. KEAY, K.C. KENDALL, AND C.T. ROBBINS. 1997. Constraints on frugivory by bears. *Ecology* 78:1105–1119.
- WILLSON, M.F., AND K.C. HALUPKA. 1995. Anadromous fish as keystone species in vertebrate communities. *Conservation Biology* 9:489–497.
- WORTON, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.
- YAMAZAKI, K., C. KOZAKAI, S. KOIKE, H. MORIMOTO, Y. GOTO, AND K. FURUBAYASHI. 2012. Myrmecophagy of Japanese black bears in the grasslands of the Ashio area, Nikko National Park, Japan. *Ursus* 23:52–64.

Received: 29 September 2010

Accepted: 20 September 2011

Associate Editor: R.B. Harris